Mutualists with attitude: coevolving fig wasps and figs

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The intimate mutualism between fig wasps and figs has long captivated biologists, and new phylogenies are now uncovering its evolutionary history. Fig-pollinating wasps evolved just once, but fig parasitism has evolved repeatedly and convergently. Figs and their pollinators appear to have co-speciated considerably, but not invariably, because the famous one-to-one rule of specificity is often broken. Some key traits of figs and pollinators show impressive correlated evolution, but the resolution of conflicts that threaten the stability of the mutualism remains controversial.

There are > 750 species of figs worldwide [1], making *Ficus* one of the largest genera of land plants. Figs are defined by a unique enclosed inflorescence, the syconium, which is also the arena for interactions with fig wasps. According to the 'one-to-one rule', each fig has its own pollinating wasp species from the family Agaonidae (Box 1), upon which it depends for pollination [2,3]. In turn, the wasp depends upon the fig for reproduction, because its larvae feed by galling fig flowers. However, there is also considerable diversity in this dynamic mutualism [4–9]. For example, some figs are monoecious, whereas others are functionally dioecious (Box 2), whilst some agaonids pollinate actively and others passively. The reproductive interests of the mutualists are not always aligned, leading to conflicts that threaten the stability of the mutualism [4–12].

Recent progress, especially in phylogenetics, has improved our understanding of the patterns of evolution and coevolution of figs and fig wasps. Integrated studies of this model system now provide excellent opportunities to probe general issues [11,13–15], such as how mutualisms persist when there are conflicts between partners, how the effects of parasites are limited, and what aspects of species associations influence the degree of co-speciation.

Origins and radiation of figs and fig pollinators
Several recent studies have estimated the phylogenies of figs and fig-pollinating wasps with the use of DNA sequences [16–20], or with a combination of molecular and morphological data [21,22]. All support the monophyly of fig-pollinating wasps, and indeed of figs, implying that the mutualism arose just once. Machado *et al.* [18] used DNA sequence divergences, calibrated with a 25-million-year-old

fossil fig wasp (of the extant genus *Pegoscapus*), to suggest that the mutualism arose ∼87 million years ago.

Co-speciation of figs and agaonids has long been suspected, but only investigated recently. Strict co-speciation should result in essentially identical phylogenies for the two lineages, whereas host shifts can cause discrepancies. Figs comprise a single genus (*Ficus*), with four subgenera and 18 sections, whereas pollinating wasps comprise a family (Agaonidae), containing 20 genera. Mapping fig sections onto a molecular phylogeny of wasp genera [18,22], or vice versa [21], has demonstrated strong conservation of host associations at this taxonomic level. However, a stronger test of co-speciation is provided by statistical comparison of two phylogenies – representing matched pairs of fig and agaonid species. This approach has been used recently [23] to demonstrate significant co-speciation of pollinating *Ceratosolen* species with their host figs (section *Sycomorus* species) (Fig. 1).

Host specificity: a pollinator paradigm postponed?
Most biologists 'know' that each fig species has a unique pollinator. However, this 'one-to-one rule' is a seductive paradigm and little energy has been expended on actually testing it [24]. Some exceptions are well established [24–26], but others might be attributable to errors, either by wasps or by taxonomists [1,3,24,25]. The role of taxonomy is self evident, but repeated sampling is also crucial to the detection of specificity breakdown [24] (Box 3). Unfortunately, the expectation of host specificity has limited the motivation to do this [24].

Wasp species can be difficult to distinguish and only 300 pollinators have been described, compared with 750 figs [3]. However, fig species can also show great intraspecific variability [3], making species delimitation difficult. Once morphological taxonomy is stabilized, molecular markers should be used to study morphospecies, because cryptic species might occur in agaonids and/or figs (Box 3).

A survey of published records suggests that it is more common to find two pollinator species per fig species than vice versa [25]. However, detailed studies of 12 species in each of the sections *Sycomorus* [20] and *Malvanthera* [19,20,27] are better controlled for taxonomy and sampling and might provide a better index of the frequency of exceptions. Six of these 24 fig species have two (or more) pollinators, whereas three out of 24 agaonids are associated

Box 1. Fig-pollinating wasps

The life of fig-pollinating wasps is bound intimately to the syconia (inflorescences) of their host figs (Fig. I). Most agaonid species pollinate only one fig species and specificity is maintained by responses of the wasps to fig volatile cues [60,61]. Female wasps enter receptive syconia through a narrow tunnel called the ostiole and then pollinate the female flowers. However, they also oviposit into some fig ovaries (Fig. Ic), which are galled by the wasp larvae. Few foundresses enter each syconium, because the ostiole closes after wasp entry, and they live for only a day or two inside their 'tomb blossom'. The wasp larvae and fig seeds then develop for several weeks. Male wasps hatch first and use their extensible genitalia to mate with females, who are still within their own galls. The male flowers are also now mature, so that the wasps acquire pollen before dispersal. The wingless male wasps bite holes through the syconium wall, enabling the females to disperse and search for new, receptive syconia.

Many aspects of agaonid biology reflect the association with figs. Males have no wings, short antennae and reduced eyes that befit their brief lives in the dark, enclosed spaces of the syconium (Fig. Ia). By contrast, females have elongate heads, easily detached antennae and wings, and mandibular appendages that they use to progress down the ostiole (Fig. Ia,b). Convergent adaptations for ostiole entry are shown by some parasitic wasps [62] (Fig. II).

The syconium also imposes strong population structure on the pollinators and, because few foundresses enter each syconium, there is local mate competition, resulting in female-biased pollinator sex ratios [63]. This is beneficial to the fig, because only female pollinators carry pollen.
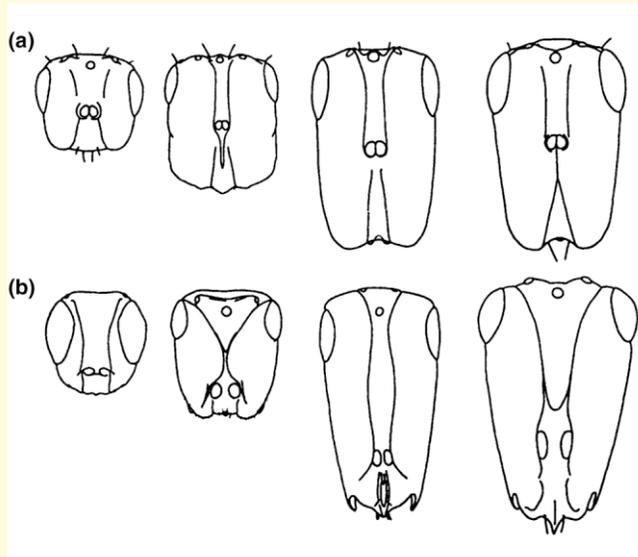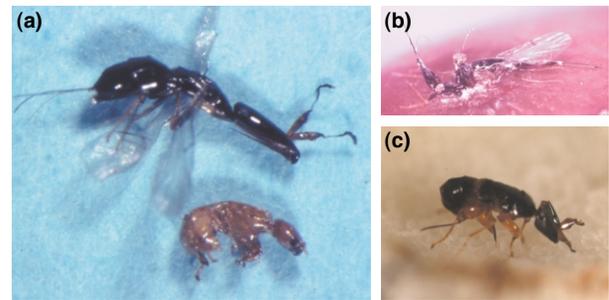

Fig. I. Fig-pollinating wasps. (a) Extreme sexual dimorphism (female above) in *Pleistodontes froggatti*; (b) *P. froggatti* females attempting to enter a receptive syconium through the ostiole; (c) *Ceratosolen josephi* foundress laying eggs inside a receptive syconium. Photographs reproduced with permission from J.M. Cook (a), D. Bean (b) and J-Y. Rasplus (c).

Fig. II. Convergent adaptations in pollinating and nonpollinating fig wasps. Pairs of pollinating (a) and nonpollinating (b) wasps that are distantly related, but enter the same syconia, have remarkably similar head shapes [62]. Figure reproduced, with permission, from [62].

with two figs [19,20,27]. On balance, it looks like the one-to-one rule might be broken in about a third of all cases.

Patterns of association might provide clues to the speciation mechanisms of the mutualists and their degree of linkage. The most common form of specificity breakdown involves two wasps with different geographical distributions [3,25], suggesting that pollinators speciate more rapidly, probably under geographical isolation, than do figs. This could result from differential trajectories of adaptive (co)evolution or genetic drift. Lack of fig speciation might
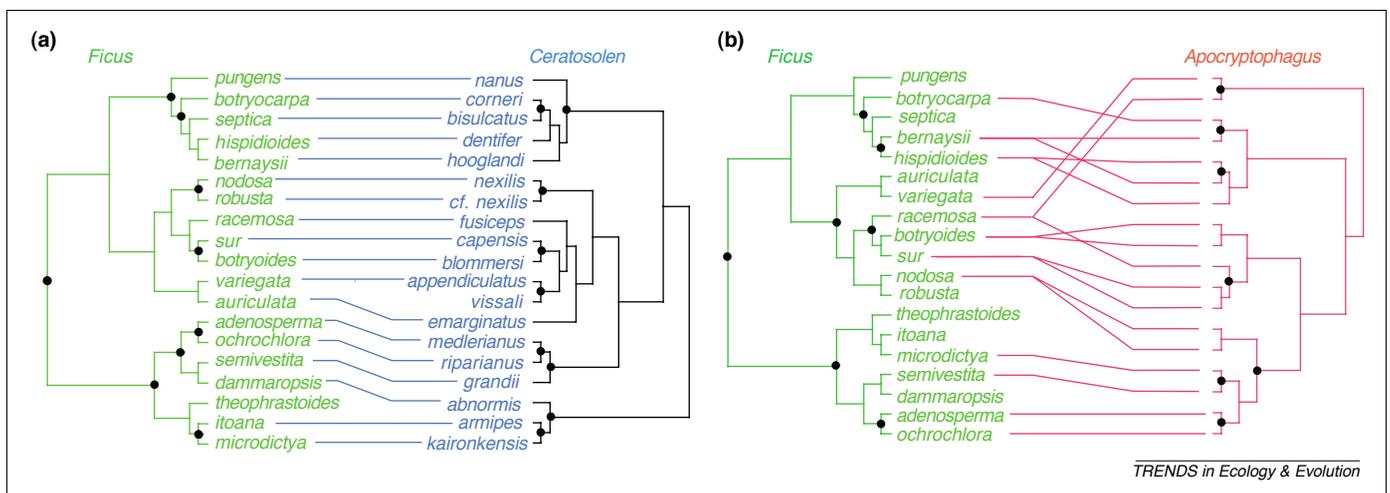

Fig. 1. Co-speciation of figs and their pollinators. Statistical comparisons reveal significant congruence between phylogenies of *Ceratosolen* pollinators (a) and their host figs, but not between *Apocryptophagus* gall-inducing parasites (b) and the same host figs [23]. Lines link wasps to their fig hosts whilst circles indicate nodes implied to have co-speciated in a maximum co-speciation analysis. Figure modified, with permission, from [23].

Box 2. Diverse ways to be a fig

The defining feature of *Ficus* is the syconium. Depending on the species, this enclosed inflorescence varies in ripe size from a pea to a tennis ball and contains from <10 to >10 000 unisexual staminate (male) and carpellate (female) flowers. In most species, syconia are roughly spherical or cylindrical, but there are hidden differences within. For example, the flower stigmas of actively pollinated figs form an attached synstigma layer, which is absent in passively pollinated species [33].

Syconium production is generally synchronous within a tree, but is asynchronous among trees. Because emerging pollinators must find receptive syconia quickly, wasp population persistence requires continual availability of receptive and mature syconia [6]. This pattern is modified in some species in which young and older syconia occur simultaneously on the same tree, and is more complex in dioecious species, where female trees are wasp 'sinks' [6].

The description in Box 1 is true for monoecious figs, in which all syconia are similar and produce both wasps and seeds (Fig. Ia).

However, about half of all fig species are functionally dioecious, with separate male and female trees [1,33]. Male syconia contain male and female flowers and produce many wasps, but few if any seeds (Fig. Ib). By contrast, female syconia contain only female flowers and produce only seeds (Fig. Ic). Male syconia contain short-styled flowers that are accessible to wasp ovipositors, whereas female syconia contain long-styled flowers that are not. In addition, male flowers are concentrated around the ostiole in dioecious figs but dispersed around the syconium in monoecious species (Fig. I). Figs exploit most warm habitats and have several growth forms (Fig. II). About half of *Ficus* species are free-standing trees, but the hemi-epiphytic 'strangler' species are perhaps more famous. Some (rheophytic) species live in streams, whereas other species occur in arid habitats as lithophytic 'rock-splitters', or along seasonal watercourses. Depending on the species, syconia can be borne on the branches, the trunk (cauliflorous) and/or on underground runners (geocarpic) (Fig. II).
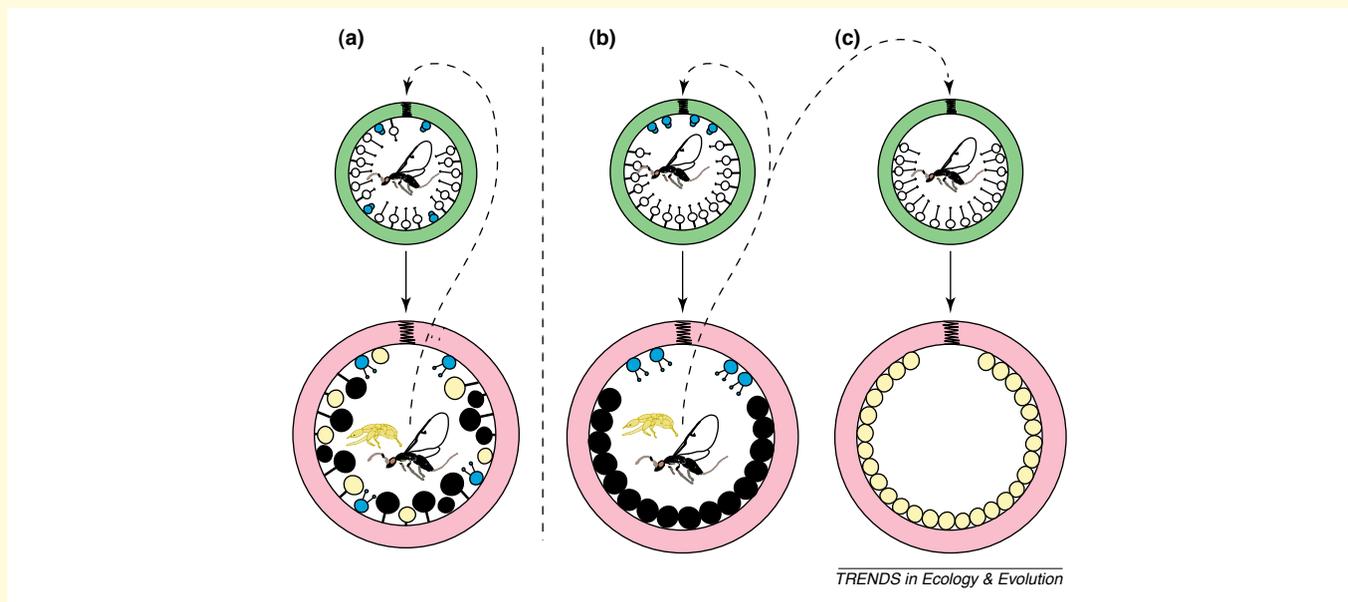

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Fig. I. Two ways to be a fig. Syconia develop from small receptive forms (green) to larger ripe ones (pink). In monoecious species (a) all syconia are essentially the same and produce both wasps (black) and seeds (yellow). In dioecious species, male syconia (b) give rise only to wasps, whereas female syconia (c) nurture only seeds and contain no male flowers (blue).

Fig. II. Examples of variation in figs: (a) *Ficus brachypoda*, a monoecious arid zone lithophyte; (b) *F. crassipes*, a monoecious rainforest strangler with cylindrical syconia; (c) *F. variegata*, a dioecious rainforest species with spherical, cauliflorous syconia; (d) Ripe red syconia of *F. obliqua* are eaten by many birds, including the rainbow lorikeet, which disperse seeds. Photos reproduced with permission from J.M. Cook.

be attributable to their ~100 times longer generation time, or to other factors, such as population size and gene flow. Although both fig and wasp gene flow are mediated by wasp dispersal, fig gene flow also depends on seed dispersal by frugivores. There are many alternative speciation scenarios, but a valuable first step is to ascertain whether co-pollinators are sister species, suggesting speciation on the current host plant, or whether they are more

distantly related, suggesting host switching. There is already support for both modes, but there are insufficient cases with which to generalize (Box 3). Host switching will be constrained by various physical, chemical and behavioural traits, which are likely to increase with taxonomic distance. Consequently, that most reports of co-pollinators involve congeneric species does not, in itself, imply speciation on the current host plant. Similarly, the

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Box 3. Case studies of specificity breakdown

The one-to-one rule of fig pollinator specificity is often assumed rather than tested. The case studies here could evolve further, but already illustrate the importance of taxonomy and repeated sampling. Unfortunately, although ecological and evolutionary studies of fig wasps have been increasing steadily for several decades, taxonomic effort has not kept up [3].

Ficus obliqua in Australia

It was long thought that *Pleistodontes imperialis* pollinated *Ficus obliqua* var. *petiolaris* and that *P. greenwoodi* pollinated *F. obliqua* var. *obliqua* [2]. However, recent revision of fig taxonomy using ordination analysis indicated that *F. obliqua* var. *petiolaris* belonged within *F. rubiginosa*, which is associated only with *P. imperialis* [64]. Thus, better taxonomy removed the exception. However, the story was unfinished. *Ficus obliqua* is widespread in eastern Australia and, although collections from most of its range consist of *P. greenwoodi*, recent sampling in northern Queensland revealed a different (and new) species, *P. xanthocephalus* [27]. *Pleistodontes xanthocephalus* and *P. greenwoodi* might be sister species, but appear to have very different geographical distributions.

Complex host associations of African Ceratosolen wasps

Ficus sur has three pollinators with different geographical distributions. Two (*Ceratosolen silvestrianus* and *C. flabellatus*) coexist in West Africa and one of these (*C. flabellatus*) coexists with the third species (*C. capensis*) in east Africa. Molecular data suggest that the two West African wasps are sister species, but it is unclear whether the third species is their next closest relative [20].

Different problems are posed by *F. sycomorus* and *F. mucuso*, which, apparently, are both pollinated by *C. arabicus*. However, *C. arabicus* specimens from different localities show unexpectedly high DNA sequence divergence, more typical of the genetic distances between agaonid species [18,20], suggesting the existence of cryptic species. Both figs also host the 'cuckoo' species *C. galili*, which does not pollinate. Morphological, behavioural and molecular evidence suggests that *C. galili* is not closely related to *C. arabicus* and has probably reached its current host figs through a series of host shifts [18,20].

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association of most genera of wasps with a single section of figs can also be explained through constrained host switching, which is why species-level phylogenies are needed to demonstrate co-speciation (Fig. 1).

Active pollination

Most insects pollinate passively, but fig wasps [28], yucca moths [29] and senita moths [30] have evolved sophisticated active pollination. Some agaonid species pollinate passively, carrying pollen dispersed on their bodies and lacking specialized behaviour. Others actively use coxal combs (on their legs) to collect pollen into special thoracic pollen pockets and later deposit it into receptive flowers [28,31]. Recent phylogenies [18,22] strongly support a basal position for *Tetrapus*, one of only two agaonid genera to lack pollen pockets. Because all other genera include at least some active pollinators, an ancestral state of passive pollination, followed by a single switch to active pollination has been proposed [18,28]. However, five out of 20 genera contain both passive and active pollinators, suggesting several secondary losses of active pollination [28].

Does active pollination benefit figs through 'economization' on pollen production? Kjellberg *et al.* [28] compiled direct observations of pollen-loading or deposition behaviour, or of pollen concentrated into pollen pockets,

for 88 agaonid species. In addition, the presence of pollen pockets and coxal combs was noted. This revealed an almost perfect correspondence between active pollination by wasps and low anther:ovule ratios in figs. It also showed that coxal combs always indicated active pollination, allowing inference of pollinator behaviour for a further 54 species (Fig. 2). Interestingly, however, pollen pockets are imperfect indicators of behaviour, because of phylogenetic inertia. For example, *Ceratosolen galili*, the only passive pollinator in a clade of active pollinators, has large (although unused) pollen pockets, but lacks coxal combs.

Active pollination is good for figs, but is it good for wasps? Pollen collection and deposition must have time and energy costs, so counter-balancing benefits are expected [6,28]. Several species of active pollinators preferentially lay eggs in pollinated flowers [6,28,32–34] and recent studies [32,34] have shown that lack of pollination can decrease the number of wasp offspring that develop successfully, possibly because of low success in gall initiation [34]. Interestingly, this could serve as a 'sanction' by which the figs ensure pollination. Such sanctions could also have a role in stabilizing other mutualisms (e.g. legumes and rhizobial bacteria) in which multiple symbiont lineages colonize each host, creating competition between symbiont lineages. However, the larvae of passive pollinators often develop in unpollinated flowers [32,34] and it seems probable that the benefits of active pollination to wasps vary considerably among species.

Keeping wasps in check

Agaonids insert their ovipositors into flower styles and oviposit into fig ovaries (Boxes 1,2). Each flower can produce either a seed or a wasp, so there is a fundamental
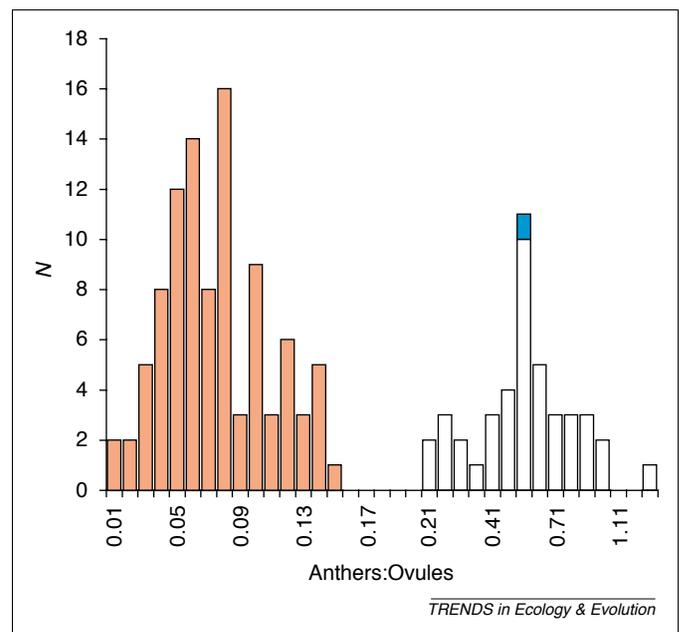

Fig. 2. Correlated evolution of pollen investment and pollination behaviour across fig species. Species with an anther:ovule ratio of <0.16 have active pollinators (red bars), while those with >0.21 have passive pollinators (clear bars). *Ficus macrophylla* (blue) is a possible exception. Its ratio of 0.53 suggests passive pollination, and indeed the pollinator has no coxal combs. However, it does have pollen pockets [27], containing concentrated pollen (F. Kjellberg, pers. commun.). Figure modified, with permission, from [28].

tradeoff between seeds and wasps [8,12]. However, there is selection on wasps to maximize reproductive success by laying eggs in as many flowers as possible, so how has the mutualism remained stable for ~87 million years?

Dioecious figs 'rear' wasps and seeds in different types of syconium (Box 2) and agaonid ovipositors are too short to reach the ovaries of the long-styled flowers of seed syconia [35,36]. The situation is more complicated in monoecious figs, because style length distributions are unimodal with most (or all) ovaries apparently accessible to pollinator ovipositors [6,9,13,37,38]. The observation that *Idarnes* nonpollinating fig wasps (NPFW) gall the same inner layer of flowers as do pollinators led to the proposal that only a subset of flowers will support wasp development, with others being 'unbeatable seeds' [39]. However, some Old World NPFW species are concentrated in outer flower layers [38,40,41], so this could not be a ubiquitous mechanism. In addition, although morphological differences between fig ovaries in male and female syconia of dioecious figs might influence wasp development [33], no such dimorphism is known in monoecious figs [10].

Even if all flowers can support wasp development, some might not be accessible. Various scenarios [42,43], including high costs for long ovipositors [43], have been proposed that might result in ovipositors that are too short to exploit all flowers, but none has significant support. Abortion of overexploited syconia could select against long ovipositors; however, although selective abortion occurs in *Yucca*, there is no evidence for it in figs [9,11]. Nevertheless, style and ovipositor length are highly correlated across 11 fig–pollinator pairs and wasp exploitation of flowers is predicted well by a comparison of style length distributions with wasp ovipositor lengths within three species investigated further [38].

Flower exploitation could be limited by the number of eggs (and therefore the number of foundresses) entering syconia [4,37,38,42]. Counts of eggs and foundresses show that this applies in several African fig species [38], but not in other cases [11,42]. There is also limited evidence that foundress number increases with syconium size both within [44] and between [4] fig species, which might suggest fig 'control' of foundress number to ensure pollination without overexploitation [4]. This would oppose the general expectation that the mutualist with the shorter generation time (wasp generations are ~100 times shorter than are fig generations) might be at an advantage in conflict situations [5,11].

Several lines of evidence suggest that foundresses preferentially exploit shorter styled flowers [10,38–40,45]. For example, in two species [38], the style length of occupied flowers increases with the number of pollinator larvae, suggesting that longer styled flowers receive more eggs as competition for oviposition sites increases. Oviposition in short-styled flowers might be less costly and/or impart higher offspring fitness. In *F. microcarpa*, female pollinators developing in long-styled flowers are smaller and later to mate and emerge [10].

Because no one hypothesis appears generally adequate, Anstett [10] suggested a two-step process whereby insufficient eggs limit exploitation in syconia with one or two foundresses, whereas ovipositor length provides the upper limit in multiple foundress syconia. It is also possible that stability mechanisms might differ among species [10,11,38].

Dioecy is different
Figs either produce wasps and seeds in the same syconia (monoecy), or in separate male and female syconia on different trees (dioecy) (Box 2). Phylogenies support monoecy as the ancestral system, with multiple origins of dioecy and some subsequent reversals [1,18,21]. Many aspects of fig–pollinator–parasite interactions differ under dioecy.

Why commit reproductive suicide?
An extra fig–pollinator conflict exists under dioecy [46]. Figs need agaonids to enter both types of syconium, but agaonids can only produce offspring in male syconia (Box 2). Consequently, there is selection on agaonids to discriminate between male and female syconia and on figs to prevent this through sexual mimicry [46]. In the edible fig *F. carica*, there is little opportunity for discrimination, because of the different seasonal phenology of male and female trees [47]. However, male and female syconia occur simultaneously in the tropical species *F. hispida*, yet discrimination appears to be absent [48]. In this species, tree density is low, so there might be selection to enter the first syconium found. Indeed, there might be general 'selection to rush' because agaonids live for only 1–2 days [6,47,48]. Interestingly, although equal numbers of wasps arrived at male and female *F. hispida* trees, the number of foundresses entering female syconia was higher, in line with fig rather than wasp reproductive interests [36]. Experiments on this topic are difficult to both control and replicate adequately, and further studies are needed.

Dioecy and parasitism
The separation of sexual function could facilitate exclusion of NPFW from seed syconia, because there is no need to enable the development of pollinator larvae, and it is indeed rare to find any wasps developing in seed syconia. It has also been argued that dioecious figs have fewer NPFW species because they have fewer flower layers than do monoecious figs, reducing the number of niches [49]. Existing data do suggest that dioecious figs have fewer parasite species [49], but the reason why is less clear.

A different idea proposes that seed syconia are parasite 'sinks' [35], reducing percentage parasitism of gall syconia, because NPFW waste time and/or eggs on seed syconia. Field data for *F. hispidoides* suggest that female NPFW do not discriminate between male and female syconia [35]. Although such processes might suppress parasitism, they occur at the population level and so will not select for transitions to dioecy.

Nonpollinating fig wasps
Similar to other mutualisms, the fig–pollinator association is exploited by parasites [14,39,40,50–53]. One fig species can host up to 30 diverse NPFW species [51,52] and these closed communities (Box 4) could provide valuable model systems for community ecology [41,51,52]. Within the syconium, niche space might be partitioned via different subsets of flowers [40,49], or timing of oviposition [23,41], as well as by larval diets (Box 4). Explaining

species coexistence in the richest communities appears challenging; however, fig wasp communities might be generally unsaturated [51,52].

NPFW species can be split into functional groups [11,41,53], which are apparent to field workers in different continents, although the species involved are different:

- Large gall-inducers and their parasitoids: these wasps are much larger than agaonids and oviposit from outside the syconium, at or before pollination. They induce large galls (or parasitize large gallers) and occur in few syconia at low numbers.
- Small gall-inducers: these also oviposit from outside, at or mostly after pollination, but the wasps are a similar size as the pollinators. They occur in many syconia at medium to high numbers and there are often many species per fig species.
- Internal parasites: these occur only in the Old World and enter figs along with the similar sized pollinators. They are found in few syconia, but occur in high numbers when present.

If parasites exploit flowers destined to be seeds/pollinators, there should be a tradeoff between numbers of parasites and seeds/pollinators. However, there are often few parasites per syconium [40,50] and their impacts can be obscured by the important consequences of variation in pollinator foundress number and resource availability [9,39]. For example, a tradeoff between *Idarnes* wasps and pollinators was only detectable when controlling for foundress number [39].

Why do figs not exclude NPFWs? Perhaps because defences might also exclude necessary pollinators. For example, some parasites use the same cues as pollinators (Box 1) to oviposit at the same time [39,40]. Many NPFWs oviposit later, but defences against these might tradeoff against attracting frugivores to disperse seeds [5,13,53].

A 'one-to-one rule' for nonpollinating fig wasps?

Studies of NPFWs are hindered by poorly developed taxonomy (Box 4), and we have little idea how many species each genus contains. Most genera parasitize only a

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Box 4. How to be a nonpollinating fig wasp

Most fig wasps are not agaonid pollinators, but how often has fig parasitism arisen and what do nonpollinating fig wasps (NPFWs) eat?

Origins and radiation

Most fig wasps belong to the large hymenopteran superfamily the Chalcidoidea [65]. Most chalcidoids that are not associated with figs are parasitoids, but the closest relatives of fig pollinators are not known [65,66]. The origins of chalcidoid NPFWs are also unresolved and their classification has changed many times [65,66], with five subfamilies recognized currently (Table I). A recent molecular study supports several independent colonizations of the syconium habitat by different chalcidoid lineages [65,66], but the details require further clarification. Nevertheless, most NPFW lineages are not closely related to the pollinators and have evolved convergent adaptations for syconium life [66]. These include long ovipositors to penetrate the syconium (Fig. I) from outside and male aptery (winglessness) to facilitate movement within the syconium. Even the key agaonid habit of entering the syconium has arisen independently in several parasite lineages [66].

Larval ecology

Some NPFW species induce galls that can prevent abortion of the syconium, even if it remains unpollinated [50–53]. Galling is probably the predominant larval lifestyle and is often suggested by rare syconia that contain NPFW but no agaonids or seeds [50–53]. Other species might be seed eaters, inquilines or parasitoids, but there is a lack of direct evidence. No species has been shown conclusively to be a true parasitoid, although patterns of co-occurrence are often suggested [53–69]. Direct investigation of larval diet in a member of one genus (*Philotrypesis*), often considered to be a parasitoid, suggested that it was in fact a cleptoparasite that laid eggs into flowers galled by pollinators, but fed on plant rather than insect tissue [70]. More direct studies of larval ecology through the dissection of galls and observation of larval habits are urgently needed. Another possibility is to allow NPFW to oviposit in syconia entered by sterilized and/or pollen-free agaonids.

Table I. Biology of the major groups of fig wasps

Subfamily (family)	Larval ecology	Oviposition	Males
Epichrysomallinae (unplaced)	Induce large galls	Most external but a few internal	Winged, very rarely wingless
Sycophaginae (unplaced)	Gall inducers	Most external but a few internal	Winged, wingless or dimorphic
Sycoecinae (Pteromalidae)	Gall inducers	All internal	Winged
Sycoryctinae (Pteromalidae)	Biology poorly understood, inquilines, possibly parasitoids	All external	Winged, wingless or dimorphic
Otitesellinae (Pteromalidae)	Gall inducers	Most external but a few internal	Wingless
Agaonidae	Gall inducers	All internal	Wingless

Fig. I. Diversity and adaptation in fig-parasitic wasps: (a) long ovipositors in externally ovipositing *Apocrypta robusta* and (b) *Philotrypesis caricae*; (c) *Sycomacophila* sp. a large gall inducer with a concealed ovipositor; (d) externally ovipositing *Platyneura* wasps exposed to predation by *Oecophylla* ants. Reproduced with permission from J-Y. Rasplus.

subset of *Ficus* sections, but do most species specialize on a single *Ficus* species? This question influences estimates of fig wasp biodiversity greatly. Recent studies of two distantly related genera (*Idarnes* and *Sycoscapter*), each associated with a particular section of figs (*Americana* and *Malvanthera*), found that each fig species tends to have a genetically distinct NPFW species [17,19]. However, host specificity might vary between taxa depending on larval ecology (e.g. gall-inducer or parasitoid) or timing of oviposition. *Idarnes* and *Sycoscapter* phylogenies also show greater than random congruence with the phylogenies of their associated pollinators, suggesting some co-speciation, or similar resource tracking [17,19]. However, a recent comparison of the phylogenies of *Apocryptophagus* gall-inducers with their *Ficus* hosts did not detect significant phylogenetic congruence [23]. Host shifts might be easier for externally ovipositing NPFW because they are not subject to the physical matching required to enter receptive syconia, which vary greatly in size and form between species [19]. In addition, although at least some agaonid larvae benefit from developing in pollinated flowers, this might not apply to many NPFWs [23]. Interestingly, sister species of *Apocryptophagous* exploiting the same host *Ficus* have significantly larger differences in ovipositor length (an index of the syconium size when attacked [23,41]) than do sister species on different host plants. This suggests a role for sympatric niche divergence in some cases of NPFW speciation [23].

So who are you calling a parasite?

The agaonid habit of entering syconia is a pre-requisite for pollination. This behaviour has also evolved in some NPFW lineages (Box 4) and new data suggest that some nonagaonid wasps can be effective pollinators [54]. Female *Diazella* wasps (subfamily Sycoecinae) emerge from *F. paracamptophylla* syconia carrying at least as much pollen as the 'official' agaonid pollinator. Furthermore, they pollinate effectively when alone and, in syconia entered by both species, their combined number is the best predictor of pollination success [54]. This and a similar second case [54] both involve figs with passive agaonid pollinators; however, there is some evidence that interlopers have a negative impact on actively pollinated figs [55,56]. Perhaps the loss of active pollination in some agaonid lineages has altered the balance such that figs can benefit from accessory pollinators, re-inventing the mutualism with a second partner.

Avoiding tunnel vision

It is easy to become fixated on the fig–pollinator interaction, but other interactions also influence both partners. For example, although fig pollen flow depends on agaonids, seed dispersal depends on frugivores [5,11] and the colour, scent and size of ripe figs is correlated with predominantly bird or bat dispersal [57]. Similarly, in dioecious figs, ripe seed syconia (requiring dispersal) are generally larger and more palatable than gall syconia [58] (but see ref 29). As another example, ants tending homopteran bugs on fig plants can modify interactions within the syconium by predating externally ovipositing NPFWs [59].

Box 5. Outstanding questions

- How is the stability of the mutualism maintained in different fig–pollinator pairs?
- How have key fig and wasp traits evolved and coevolved during their phylogenetic history?
- Is fig and/or pollinator speciation driven by forces intrinsic to the mutualism or by other factors?
- How can two pollinator species coexist on the same fig species, and how often does this occur?
- Are co-pollinators usually sister species?
- How common are cryptic fig and/or wasp species?
- Who eats what in nonpollinating fig wasp communities and how are these communities structured?

Conclusions

There is increasing support for the traditional view that figs and agaonids have highly correlated speciation histories. However, the famous one-to-one rule is often broken, suggesting that fig and pollinator speciation is not always tightly linked. Many fig-parasitic wasps might be as host-specific as the pollinators, but host (and niche) shifts probably play a greater role in their speciation. Comparative studies are beginning to explore how key traits have (co)evolved as figs, pollinators and parasites have radiated, but the stability of the mutualism remains controversial and mechanisms might differ between lineages. Important questions remain (Box 5) and, when addressing them, it will be crucial to consider biological differences among different fig and wasp species.

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