Figs and fig pollinators: evolutionary conflicts in a coevolved mutualism

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Figs and fig wasps form one of the best known examples of species-specific mutualism and coevolution. Recent experiments and observations have led to a better understanding of the evolutionary processes involved in the origin and maintenance of species interactions. The observed fine-tuned traits involve not only coevolution but also selection acting on only one of the partners. Furthermore, some of the 'fine-tuned traits' appear to be preadaptations – traits that existed before the mutualism was established.

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Mutualisms are interspecific interactions benefiting all the associated species. Studies of mutualisms in a cost/benefit perspective[1] highlight the difference between the traits involved in the cooperation which benefit the individual and those which only benefit the group (often counterselected). Conflicts between mutualists seem to be omnipresent and there is a continuum from positive (mutualism) to negative (e.g. parasitism, predation) interactions[2,3]. Conflicts between mutualists are often viewed as limiting evolution towards a higher benefit for both partners. For example, one partner might do best if the other is completely specific, while selection may act on the other partner for limited specificity. These conflicts have also been seen as forces destabilizing the interaction, possibly leading to drastic changes in its outcome, notably in the event of changes in environmental conditions[2]. Why these conflicts do not disrupt extant mutualisms is largely unknown.

To distinguish between general patterns in the evolution of interacting species and patterns unique to a single interaction, a comparative approach is needed. With some 750 pairs of species[4] (Box 1) exhibiting large variations in life history traits, the mutualism between fig trees and their pollinating wasps facilitates this approach. Moreover, the interaction is species-specific[5], and the costs and benefits of the interaction are readily expressed in numbers of offspring.

After a brief description of the natural history of this mutualism, we will contrast the two kinds of fig–wasp mutualisms. We will then review the different conflicts and constraints central for the stability of these mutualisms with current hypotheses on their evolution.

Fig trees (*Ficus*, Moraceae) are tropical and subtropical trees, shrubs or vines. Generally, each species is only pollinated by its own species of pollinating wasp (Hymenoptera, Chalcidoidea, Agaonidae, Agaoninae) which can only breed in female flowers of its specific host[5] (Box 1). Fig tree flowers are enclosed within a closed urn-shaped inflorescence called a 'fig' or a 'syconium' (Fig. 1). The female, pollen-transporting wasp (or foundress) enters, pollinates, lays eggs in the ovary of some female flowers and, usually but not always[6], dies within the inflorescence. Each larva develops at the expense of a single fig ovary. Figs are also inhabited by a variety of non-pollinating chalcid wasps (Box 2). Several weeks after pollination, seeds reach maturity, male flowers produce pollen and the new generation of wasps is adult. After mating, female wasps become loaded with pollen of their natal fig. They then exit in search of a new, receptive, fig in which to lay eggs (see Refs 7,8 for a more detailed description). After the wasps have exited, the figs ripen and the seeds are dispersed by various frugivore species[9,10].

Because the fig–pollinator mutualism is obligate and highly specific, the life cycle of pairs of species are closely entwined, leading to an apparently perfect cooperation. However, the mutualism can also be viewed as reciprocal slavery: over their prolonged common evolutionary history, each species has been selected to exploit its obligate partner without being able to avoid being exploited. Many evolutionary conflicts between figs and their pollinators were first pointed out by Janzen[11]. It is only recently that some mechanisms responsible for the persistence of the interaction despite these conflicts have been identified.

Distinct levels of benefit define two kinds of fig mutualisms

Within the fig–wasp mutualisms, two different functionings of the interaction are characterized by different costs and benefits, and linked to the reproductive system of the tree (monoecious or dioecious). This diversity allows a comparative approach and tests of evolutionary hypotheses. Half of all fig species are monoecious: each inflorescence produces seeds, wasps and pollen. Individual fig trees are selected to breed the wasps because it is their only way to disperse pollen, while individual female wasps are selected to visit a fig because it is their only way to reproduce. The monoecious system represents one of the few mutualisms in which there is selection on both partners to cooperate. Nevertheless, monoecious figs and wasps conflict on the optimum of some traits (e.g. seed versus wasp production[12], see below).

The other fig species are morphologically gynodioecious, but functionally dioecious: half the trees are female and produce only seeds, and the other half are anatomically monoecious (each inflorescence possesses male and female flowers) but functionally male, producing pollen and pollen-transporting wasps[13]. In male figs, wasps develop within female flowers that do not participate in female function since they only very rarely produce seeds[14]. Because of a peculiar structure of the flowers of the female figs (see below), the pollen transporting wasps that enter female figs, and actually ensure seed production, cannot lay eggs and die without reproducing. Entering a female fig should thus

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be counterselected. In the dioecious system, male trees are selected to breed wasps, but pollinators should be selected to avoid female figs, that is, not to cooperate in seed production.

Monoecy is ancestral in figs; dioecy has probably originated at least twice[4] and reverted two or three times to monoecy[4,5]. Hence there may have been several shifts in selection on the wasps either in the direction of avoiding seed producing figs (in the case of dioecy) or in the direction of visiting seed producing figs (in the case of monoecy): mutualisms may evolve towards decreased as well as increased conflicts.

In both cycles, because pollen of one fig is dispersed only by the female wasps maturing within that fig, wasp production forms part of the male function of the plant, and fig trees are selected to breed wasps. Thus, *Ficus* mutualisms differ from yucca[15] and *Trollius*[16] pollination mutualisms, in which pollinator offspring also develop at the expense of seeds but leave their host plant before loading pollen[15,16], and thus do not give it any reward. Yucca and *Trollius* are selected to kill pollinator offspring, while *Ficus* are selected to breed them[17].

Box 1. Figs and their pollinators: specificity and parallel cladogenesis?

In figs, according to morphological taxonomy, 'in general, (sub-) sections of *Ficus* have recognizable groups (mostly genera) of pollinators, but exceptions do occur'[5]. Recent preliminary molecular phylogenies of figs and pollinators[42,45] at different taxonomic scales strongly suggest that strict parallel cladogenesis could indeed be the rule. Recorded instances of two pollinators regularly associated with one fig species or one pollinator with two fig species[46] could represent intermediate steps in the process of speciation. Strict parallel cladogenesis could be enforced by (1) the wasps not being capable of developing on an illegitimate host, (2) the wasps not being capable of evolving a response to the 'bouquet' of odors produced by the illegitimate host, or (3) competitive exclusion by the wasp normally associated with the illegitimate host.

In at least one case of an isolated fig species introduced without its pollinator, alien pollinators managed to develop successfully[47]. Such mismatches probably occur regularly within the natural range of fig trees, but stay unnoticed because they only represent a very small fraction of the wasp production. Hence, parallel cladogenesis is enforced either by an evolutionary constraint – the wasps cannot evolve sensitivity to an illegitimate host – or by interspecific competition – a wasp cannot outcompete the legitimate pollinating wasp. Ongoing work on fig and pollinator taxonomy, phylogenies and the pollination of ornamental figs introduced without their pollinators will rapidly shed light on short-term and long-term processes acting on fig and pollinator speciation.

Why do wasps pollinate female figs in which they do not reproduce?

In dioecious fig species, the wasps that enter female figs and ensure seed production leave no offspring. There is thus a conflict between the wasps, who have an interest in avoiding female figs, and the trees, which need visits of female wasps for pollen dispersal and for seed production. Even if in all cases we can expect that trees of each sex are selected to mimic each other, mimicry is not perfect. The resolution of this conflict seems to differ according to the phenology of the plant.

In dioecious species with within-sex synchronized flowering phenologies (e.g. *F. carica*[13] and *F. exasperata*[18]), male and female figs are very rarely receptive (and hence attractive) at the same time. Wasps emerging when female figs are receptive die without reproducing, either within or outside a female fig. Therefore, at that time, entering female figs is selectively neutral[13]. Moreover, since female figs look like male figs, we can expect that even if female wasps are able to distinguish between male and female figs, they will persist in entering female figs when male figs are not available. Thus, fig phenology acts as a constraint that prevents wasps from avoiding

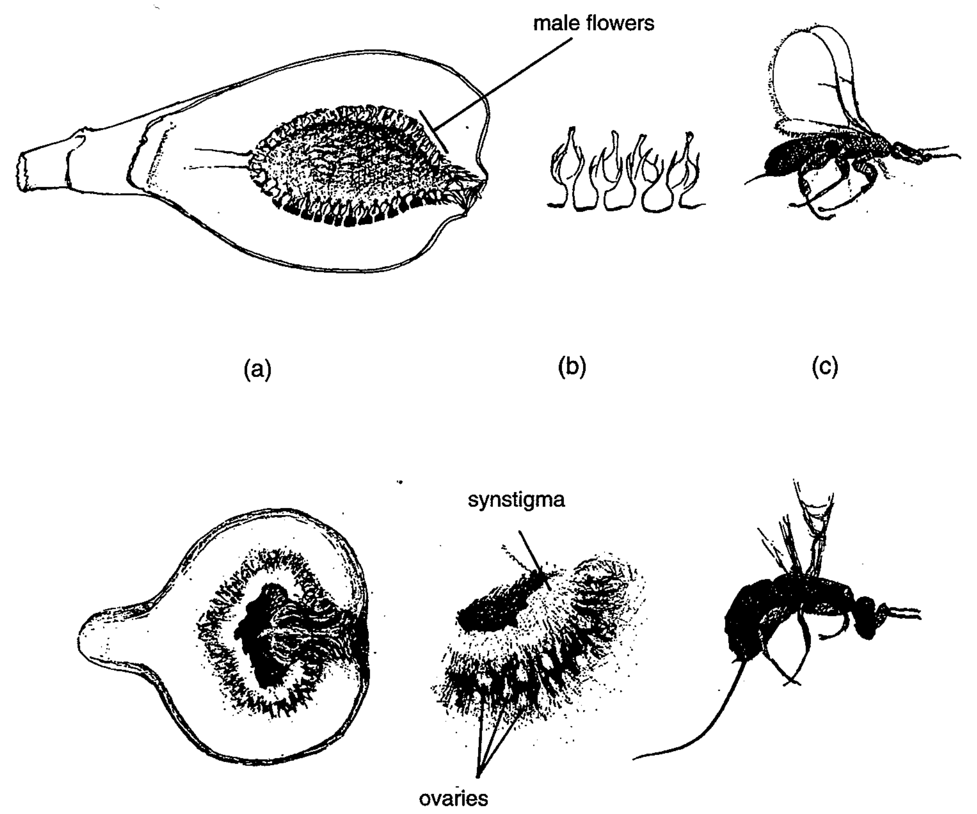

Fig. 1. Details of a receptive fig of the monoecious *Ficus racemosa* (below) and of a receptive male fig of the dioecious *F. carica* (above), with their respective pollinators, *Ceratosolen fusciceps* and *Blastophaga psenes*. (a) Whole fig in cross section. The inside of the fig is lined with female flowers. In *F. carica* there is a well-developed male flower zone, while in *F. racemosa*, male flowers are few and hardly visible at that stage: *Blastophaga psenes* gets passively loaded with pollen while *Ceratosolen fusciceps* actively collects the pollen in thoracic pollen pockets. Thus, a limited quantity of pollen is sufficient in *F. racemosa*. (b) Detail of the female flowers lining the fig. In the male fig, there is a single layer of ovaries, stigmas are well separated and styles are very short. In the monoecious fig, ovaries are disposed in several irregular layers, the stigmas and part of the styles are fused forming a synstigma, a trait common in figs of monoecious species and in female figs. In figs of monoecious species, such as *F. racemosa*, styles are longer relative to ovary size, and style length is much more variable. (c) The pollinators (females). The head is flattened to allow entry into the fig, the wings and part of the antennae may break on passing through the ostiole. In agreement with style lengths, the valves of the ovipositor are much shorter than the gaster in pollinators of dioecious figs and half as long to twice as long as the gaster in pollinators of monoecious figs (in *Ceratosolen fusciceps*, 1.5 times as long).

Box 2. Non-pollinating fig wasps: a fascinating community

While most studies focus on pollinators, figs host numerous non-pollinating chalcidoid wasps that may interfere with the mutualism[21]. Many are gall-makers, inducing the development of the ovule on which the larvae feed. These species are potentially competitors of the pollinators. The remainder use ovules already hosting another wasp larva. All non-gallers and most gallers oviposit from outside the fig, inserting their ovipositor through the fig wall to reach female flowers. However, some species of at least three subfamilies of gallers do enter the fig to oviposit[21,48], probably showing a case of recurrent evolution.

Most chalcidoids associated with figs are specific to a fig species and hence form well-defined entities, from two to 30 species for one fig. This enables (1) the study of convergences between species and (2) a comparative study of simple communities with different structures and numbers of species. For instance, all the wasps entering the fig are short-lived compared to their relatives ovipositing from the outside[21]: the short lifespan of pollinators, which limits the stability of the mutualism, is probably an adaptive consequence of entering figs. At the community level, the number of non-galler species is highly correlated with the number of galler species[21,49], suggesting some host specificity or at least preference and, to some extent, consistency in community structure. Overall, the wasp communities associated with fig trees appear to be unsaturated, maybe because they are communities of specialists[21]. Dioecious figs almost lack gallers other than pollinators and thus have a very simple organization and particularly few species, a putative advantage of dioecy in figs[50]. In the monoecious *Ficus sycomorus* lineage of supposedly dioecious ancestry[4], the composition of the fig wasp community is typical of monoecious figs[51]; the simple organization of wasp communities on dioecious figs seems to be really connected with dioecy[50].

Beyond the fundamental interest of fig-associated wasps for the investigation of hymenopteran community structure, they are providing an increasingly useful comparative tool for understanding the evolution of pollinator traits.

female figs. Whether this seasonal phenology was present before the origin of dioecy, or whether it represents an adaptation selected to prevent wasps from entering only male figs, is an open question.

In other dioecious fig species (e.g. *F. hispida*), however, male and female figs are regularly receptive simultaneously[18]. The pollinators of *F. hispida*, when given a choice, do not discriminate between receptive male and female figs, although they present external differences[19]. Wasp choice has not evolved either because wasps cannot perceive these differences (perfect mimicry of male and female figs for the cues used by wasps) or because there is no selection on the wasps to be choosy. For instance, when oviposition sites are limiting, rushing into the first located receptive fig may be favoured[19].

Hence, this conflict about entering a female fig is resolved either because intraspecific interactions (competition for egg-laying sites) represent a stronger selective force than the interspecific conflict and hence choosiness is not expressed, or by an evolutionary constraint enforced by the tree (phenology or intersexual mimicry), which prevents wasps from avoiding female figs.

Phenological constraints and survival of the wasp population

Fig flowering phenology is also central for the survival of the wasp population. Wasp larval development only lasts a few weeks[20] and adults live only one or two days[21]. When adults exit their natal fig, they have to rapidly find a new receptive fig in which to lay eggs. In *F. carica* all male trees are synchronized, producing discrete crops timed to host 2–3 successive and non-overlapping generations of wasps a year[13]. In aseasonal dioecious[18] and most monoecious species, flowering is usually synchronous within each tree (without overlapping generations) but highly asynchronous among trees, ensuring production of receptive syconia throughout the year, and thus survival of the pollinator population[11,20,22] (Fig. 2).

The selective pressures involved in the evolution of such a phenology have not been investigated. However, in seasonal locations, adaptations to ensure pollinator survival during periods when few figs become receptive have not been detected[23]: there is no selective pressure on individual fig trees to maintain the wasp population. Furthermore, flowering synchrony within trees and asynchrony among trees has been documented in Moraceae genera other than *Ficus*, suggesting that this trait existed before the mutualism[22]: it may have been a preadaptation for the mutualism.

The spread of flowering events all year round and the intra-tree synchrony of flowering allow respectively the survival of the wasp population and effective pollen dispersal. However, they raise the problem of encounter between both partners in time (there must be enough trees to provide receptive figs all year round) and in space (wasps must be able to reach the receptive trees) (Fig. 2).

Because pollinator arrivals to a crop of receptive figs usually last only a few days, fig receptivity has been assumed to be short. Models that assume short receptivity have shown that, in one monoecious species, about 100 trees are needed to maintain a wasp population for five years with a 0.5 probability of survival[20]. However, when applied to seasonal environments, these models predict huge minimum population sizes[24]. Duration of receptivity was investigated as a factor that could reduce the predicted minimum population size. A simulation model predicted that there is selection on the trees to maintain longer periods of fig receptivity (about three weeks)[24]. This result was confirmed by field experiments on two species in seasonal environments[25]. This long duration of receptivity may reflect the dynamics of the mutualism: in many situations, pollinators are sometimes scarce and receptive figs have to wait for pollinators to become available. The long duration of receptivity is a trait that could be explained by selection on the trees resulting from the mutualism. Moreover, as for flowering phenology, prolonged receptivity may have been present as a preadaptation in the anemophilous ancestors of figs before the mutualistic association began[25].

Despite prolonged receptivity, because specific densities of fig trees are often low[26], the predicted area of fig tree populations may be large[24]. Wasps must be able to locate and reach receptive figs of the right species over large distances despite their small size and lifespan. Wasps leave their natal tree downwind, probably by passive drift[27]. They reach receptive trees moving upwind, by active flight[27]. Female wasps are attracted to receptive trees (at least over short distances) by specific chemical volatiles[28] that are also responsible for the stereotyped behavior of the wasps when entering a fig[29], and probably for the specificity of the interaction (Box 1). Wasps travelling between trees carry a marker of their origin: pollen. Through paternity analysis of seeds produced by figs visited by single wasps, it has been shown that the pollen-carriers arriving on a receptive tree came from many different trees[30]. Apparently the area covered by trees that freely exchange wasps is huge, the wasps regularly covering distances of up to ten kilometers[30]. This high dispersal ability of wasps allows sustainability of the mutualism at low fig tree densities. Moreover, this may have major consequences on gene flow in fig tree populations.

Why do some wasp species pollinate actively?

In most pollination systems, pollen deposition is only a by-product of insect visit for a reward. However, when the reward is an egg-laying site with larvae feeding on developing seeds (*Ficus*, *Trollius*, Yucca), flower fertilization may enhance offspring fitness, and insects may be selected for effective pollination[31]. However, even in that case, optimum pollination for insect larvae does not necessarily coincide with the optimum for seed production. In figs, this is illustrated by the oft[12], but not always[12,32] recorded increase in seed and wasp production with the number of foundresses, which clearly shows that pollen limitation can occur.

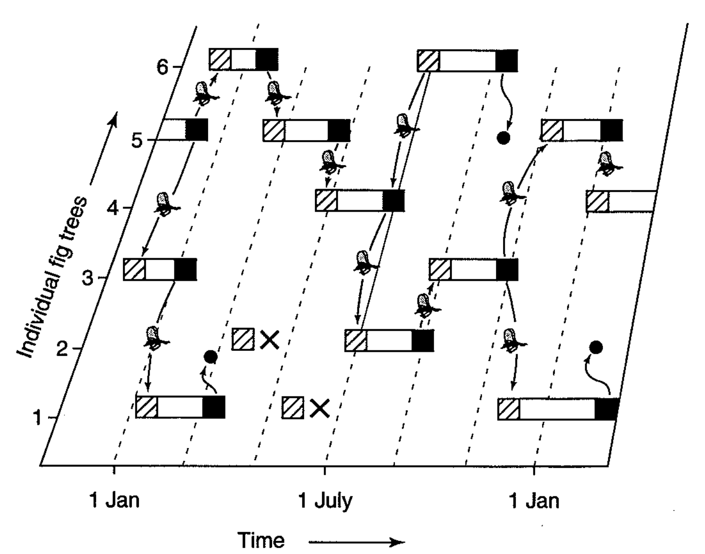

Fig. 2. Schematic representation of the successive generations of pollinators of monoecious figs. Each tree produces well-defined crops of figs at irregular time intervals (*x* axis). These crops may go through the successive phases of receptivity (hatched box), pollinator and seed development (white box) and finally pollinator emergence and fruit ripening (black box). Pollen-loaded pollinators emerge from a crop when the figs ripen (black boxes). During their short lifespan, they have to find a crop of receptive figs (hatched boxes), otherwise they die without reproducing (wasps produced by the first and third flowering episodes of tree 1 and by the second flowering episode of tree 6). If a crop is not pollinated while receptive, it aborts (first flowering episode of tree 2, second flowering episode of tree 1). Otherwise the wasp larvae and the seeds develop (white box) until the new generation of wasp emerges (black box). This functioning ensures the survival of the pollinator population when a sufficient number of trees are within flight distance for the pollinators. A by-product of this functioning is that ripe figs are available year round and may thus constitute a keystone resource for fruit dispersers.

In both monoecious and dioecious fig tree species, pollination can be either active or passive. Females of active species collect pollen from their natal fig into special structures called pollen-pockets. After entering a receptive fig, they actively deposit pollen on the stigmas while ovipositing. Females of passively pollinating species have no behaviour specifically aimed at collecting and depositing pollen. Pollen gets trapped on the body of the wasp and is incidentally deposited in the receptive fig[33]. For two active pollinators of monoecious figs and one of a dioecious fig, it has been observed that the fig embryo develops in the ovaries in which an egg is deposited[34]. This supports the idea that fertilization and endosperm development benefit larval development. The influence of effective pollination on wasp fitness is, however, known for only three species. Larvae of *Blastophaga psenes*, the passive pollinator of *F. carica*, develop normally in unpollinated figs[35], whereas pollination, while not absolutely necessary, ensures a better larval development of *Platyscapa quadraticeps*[36] and *Elisabethiella baijnathi*[7], active pollinators of *F. religiosa* and *F. burtt-davyi* respectively. Hence, active pollination is not maintained by an evolutionary constraint on the wasp – wasp larvae can develop in unpollinated figs – but by short-term selective pressures: larvae of actively pollinating species seem to do better when the fig is pollinated. If these selective pressures can be relaxed then reversal from active to passive pollination can be expected to occur. Although in most fig species the mode of pollination is undocumented, it is known that within at least four pollinator genera, some species have pollen pockets and others do not[5]. This may result from several independent instances of evolution of active pollination and reversions to passive pollination. Data on additional species and precise phylogenies are sorely needed to test the generality of this conclusion.

Regulation of the production of wasps and seeds

In monoecious fig trees, each female flower may produce either a seed or a pollinator offspring, that is, each female flower may contribute to female or male function of the tree[8,12,32]. Trees are selected to produce both seeds and pollinators. However, wasps are selected to produce as many offspring as possible. Thus, figs and wasps may conflict over the proportion of developing female flowers that will produce a seed[12,32].

Fig pollinators introduce their ovipositor through the style and deposit the egg within the ovule. In dioecious figs, the very short ovipositors of the pollinator[5] (Fig. 1) do not allow them to reach the bottom of the very long styles of flowers borne by female trees[35]. Moreover, the inner integument of the ovules is much more developed in female figs[34], a feature which could be a proximate factor prohibiting oviposition. By analogy with dioecious figs, it is often stated that monoecious figs have long-styled flowers for seed production and short-styled flowers for wasp production. This is not true. In monoecious figs, style length distribution is unimodal, and most flowers have an intermediate style length[37–39]. Furthermore, in monoecious species, all the ovules have the shortened inner integument observed in the ovules of male trees[34], that is, in ovules dedicated to wasp production. Thus, the hypothesis of a particular structure of some ovaries precluding pollinator oviposition is not borne out. Moreover, the pollinators of monoecious figs have ovipositors long enough to gain access to many more ovaries than they actually use[37,38] – up to 100% (Ref. 39). Some pollinator larvae develop in long-styled flowers, and pollination of figs by a saturating number of foundresses leads to a mean production of 80 to 90% wasps[32,38]. Thus, ovary use by wasps cannot simply be analyzed as an escalation between ovipositor and style length[37–40].

Within a fig, ovaries are densely packed into several irregular layers (Fig. 1). Since all stigmas are at the same level, flowers of the inner layers tend to have below-average style lengths, and flowers from the outer layer tend to have above-average style lengths. Pollinators preferentially lay eggs in the inner layer of ovaries[38]. Because some gall-making chalcid wasps, ovipositing from the outside of the fig (and not through the style), seem to use the same ovaries as the pollinator[40], the advantage of using short-styled flowers is not due to style length or structure but more probably to the position of the ovary relative to the lumen of the fig[32]. Galls developing near the lumen could be less space-stressed, putatively allowing a better development of larvae and/or a better access to females within these galls for mating[32]. Since the relative number of pollinator offspring produced by a fig depends on the number of foundresses that entered it[12,32,38], density-dependent phenomena must also be taken into account. The reproductive strategy of a wasp will depend on the quality of the different oviposition sites, the cost of having a longer ovipositor, and the probability of competing with other wasps for oviposition sites. Hence, a new generation of explanations is developing for why the wasps do not develop in all female flowers[41].

Conclusion

The sustainability of the fig–wasp mutualism is based on multiple biological traits of each partner. Among these traits, only a few (like the partitioning between seed and wasp production in monoecious figs) seems to clearly result from trait for trait coevolution. Other characteristics may be driven by selection on one species, the other species only adjusting to shifts in the first species. Other traits are preadaptations (e.g. flowering phenology of monoecious figs). In some of the fig–wasp conflicts, evolutionary theory predicts a breakdown of the mutualism (e.g. evolution of avoidance of female figs by pollinators of dioecious species). The mutualism is then only maintained because of an 'unbeatable' constraint imposed by one mutualist on the other (e.g. odor mimicry between male and female figs).

Up to now, studies on the fig–pollinator mutualism have mostly been limited to case studies on one or two species. A pioneer comparative research program on several American species[12,42] has nevertheless been pursued in Panama, one has started in India[39] and another in Africa[21]. With the increasing number of case studies and the ongoing developments in taxonomy and molecular phylogenetics, a global comparative approach to the evolution of the mutualism will soon be possible. It can be expected that recurrent evolution of such traits as ovipositor length, active and passive pollination, or number of parasites associated with one fig species, will be demonstrated and explained in terms of selective pressures.

Recent developments in the comparative study of the origin of mutualistic pollination in the lineage leading to yuccas have shown how such studies provide valuable insights into the origin and evolution of mutualisms[44]. Such comparative studies show that preadaptations are central in the establishment of mutualisms[43,44] . But they also canalize the mutualism, and each set of preadaptations may define a limited set of possible types of stable interactions (e.g. the differences in functioning between figs and yuccas seems to be due to different preadaptations). Nevertheless, selective pressures may change once the interaction is established and some major shifts in the selective pressures may occur (following for instance a shift from monoecy to dioecy).

Among all the species presenting preadaptations to a mutualism, only those for which the response to individual selection was compatible with the evolution and the maintenance of the mutualism have become and have remained mutualists. There is hence an inherent necessity, either for selection that circumvent the major conflicts for whatever direct or indirect reason or for evolutionary constraints, one mutualist not being able to respond to the selective pressures imposed by its partner. It is an open question whether these traits that stabilize the system (1) are direct adaptations to the mutualism, (2) are the by-products of selection on another trait, or (3) are pre-adaptations, and finally whether reversal of such traits sometimes occur leading to the breakdown of some mutualisms.

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Indiscriminate altruism: unduly nice parents and siblings

Laurent Keller

Many animals can identify their relatives and bias altruistic behaviour in their favour. However, recent studies have also uncovered cases where nepotism might be expected but is weak or absent within social groups. For instance, in some bird and mammal species, males apparently feed offspring that have been sired by other males at the same rate as their own offspring. Similarly, social insect workers fail to favour more closely related individuals within their colony. Why is this so?

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Kin recognition, defined here as the differential treatment of relatives, occurs in a large number of species (see Refs 1–3 for review). The two traditionally hypothesized benefits of kin recognition are (1) to favour fitness of more-related individuals (nepotism), and (2) to ensure an optimal balance between inbreeding and outbreeding[4]. The benefits of an efficient kin-recognition system are illustrated by the simple case of a worker ant. By helping the queen increase her reproductive success, the worker indirectly passes on to future generations copies of genes that are identical by descent[5]. The benefits of such altruism rely on the workers being related to the queen that receives the help, which indeed is the case in most species[6,7]. A common chemical label among nestmates is an important factor that maintains colony cohesion. This signature comes from a combination of genetically specified and environmentally acquired cues that are transferred among colony members. By learning the colony-specific chemical signature, workers can accurately discriminate nestmates from non-nestmates[1].

However, situations occur where nepotism seemingly ought to be favoured but is absent. Here I consider two such situations and discuss the causes that might be responsible for the paradoxical existence of indiscriminate altruism.

Nice parents

Most benefits of parental behaviour depend on the recipient of care being related to the care giver[5,8,9]. However, molecular techniques have revealed that multiple paternity is frequent in species with parental care[10]. In such a situation, the ability of a male to recognize and preferentially care for its own offspring would provide substantial benefits, yet several experiments suggest that both in birds and in mammals males appear not to assess their genetic relationship with the recipient of their care (Table 1). In addition, Kempenaers and Sheldon[11] review several studies providing indirect evidence that male birds do not exhibit kin discrimination among

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