

Ficus-pollinator research in India: Past, present and future

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Some major questions involving the species-specific mutualism between figs and their pollinators may be answered in India because of: (i) its diversity of figs and associated insects; (ii) its near-unique biogeographic position regarding fig flora; and (iii) its monsoon-dominated rainfall and its relief patterns, which together result in strong seasonality and abrupt climatic gradients.

We discuss the systematics, biogeography and coevolution of figs and wasps; ecology and evolution of fig/pollinator associates; critical population size and the effect of seasonality on the mutualism; and evolution and maintenance of the dioecious fig/pollinator system. In every case, we present questions that may be answered by appropriate studies in India.

Figs (*Ficus* spp., Moraceae) and their pollinators (Hymenoptera: Chalcidoidea: Agaonidae: Agaoninae, *sensu* Bouček¹) are partners in one of the oldest and most tightly interdependent mutualisms between insects and plants. The partnership dates back at least to the Oligocene period, around 25–30 million years ago, when ancestral wasp species are thought to have been seed predators of ancestral fig species^{2,3}. Today, there are about 750 fig species worldwide; this evolutionary radiation has been accompanied by radiation of pollinator species. The mutualism is extremely specific: each fig species is obligately pollinated by usually one wasp species, and, with few exceptions^{4–6}, each wasp species can usually only reproduce within the flowers of its single host fig species⁷.

Fig pollination systems, by virtue of their existence in ca. 750 fundamentally similar but significantly variable versions, offer many advantages as models for examining general questions in evolutionary biology⁸. First, these systems offer opportunities for studying processes of coevolution and speciation in diversifying mutualisms. Second, they furnish ample material for testing hypotheses about the evolution of sex allocation. For example, fig wasps have the ability to manipulate the sex ratios of their offspring in response to the degree of local mate competition. Figs have evolved a range of reproductive systems, including monoecy (primitive in the genus), dioecy (derived from it), and apparently secondary monoecy (reversion from dioecious ancestors)⁹. Third, because fig-pollination systems require the

maintenance of two species-specific, obligate partners, they offer useful material for studying problems of maintaining viable populations for conservation.

India is a favoured location for the study of many key aspects of fig/pollinator mutualisms. First, the country has around 60 fig species representing many sections of the genus^{10,11} and their associated insects^{12,13}. Second, India's biogeographic position results in a fig flora that combines elements historically associated with drier, more open habitats, on the one hand, and humid forest habitats, on the other. Third, India has distinct patterns of monsoon-dominated rainfall and relief that result in strong seasonality and abrupt climatic shifts over short distances. These patterns are important for fig biology, and are relevant to current research in several ways. For example, because year-round flowering is required to maintain the pollinator population, strong seasonality may impose severe constraints on the mutualism¹⁴. Also, seasonality is postulated to have played a role in the evolution of dioecy in figs¹⁵. India offers near-unique opportunities for a comparative approach to study these problems.

Systematics, biogeography and diversity of figs and fig wasps in India

Status of knowledge on systematics of figs and fig wasps

Hooker¹¹ proposed one of the first infrageneric classifications of *Ficus*; this work remains a comprehensive source of information on the occurrence and distribution of figs in India. Corner^{10,16–28} published the first major re-classification of fig taxa in tropical Asia and Australasia. His work is being revised by Berg^{9,29–31}.

The hymenopteran associates of figs include not only the pollinators, but also several groups of non-pollinating fig wasps, which appear to have undergone an explosive radiation similar to that of pollinators³². Taxonomic studies on fig pollinators and non-pollinating fig wasps began in the 1800s; Wiebes³³ provides a good historical review. Research on the systematics of fig wasps in Asia has been carried out

mainly by Wiebes^{7,33-58}. This work is being extended by others^{1,12,59-61} focusing on non-pollinating wasps. The laboratories of Joseph and Abdurahiman have produced most of the work on the species-level taxonomy of wasps associated with fig species in India⁶²⁻⁸⁸.

Much work on systematics of Indian fig wasps remains to be done. Based on the compilations of Hooker¹¹, Wiebes¹³, and Rasplus¹², pollinators of nearly half of all Indian fig species have not yet been identified and described. Evolutionary-ecological studies of these species lack a firm foundation until the systematics of their pollinators has been worked out. The situation for the non-pollinating fig wasps is similar^{12,32}. Much work remains before the figs and fig wasps of tropical Asia can be given a synoptic treatment similar to that of Berg and Wiebes⁸⁹ for the African species.

Biogeography of figs and sycophilous insects

Anatomically and morphologically, as well as in number of species, the fig flora of the Oriental and Australasian biogeographic regions is far more diverse than that of Africa or the Neotropics⁹. Diversity is especially great in the Oriental region, of which India is a part. This region is thus a favoured location for studies of the comparative biology of figs, the utility of which was underscored by Bronstein and McKey⁸. Based on distributions given by Corner¹⁰ and Berg⁹, of the 18 sections of the genus *Ficus* (including the subgenus *Sycomorus*, which is not divided into sections), representatives of 12 sections occur in India, compared with two for the entire Neotropics and six for Africa excluding Madagascar. These sections include a variety of reproductive types: monoecious, dioecious and secondarily monoecious^{9,10} whereas those in the Neotropics are strictly monoecious, and those in Africa mostly so, with relatively few dioecious and secondarily monoecious species. To some extent, these apparent differences may reflect the uneven intensity of taxonomic research on figs in different regions, but the overall pattern of greatest diversity in the Asian and Australasian tropics is likely to persist. The habitat distributions of fig species in India range from dry forest to wet evergreen forest, from rock-face to riparian; the growth forms range from scandent plants and creepers to hemiepiphytes and large, free-standing trees. This ecological and evolutionary diversity of the Indian fig flora offers ample opportunity for comparative studies of the distribution and radiation of different sections and ecological types of the genus *Ficus*.

Fig pollinators are but one group of fig wasps (sycophilous wasps). The current classification of the pollinators (subfamily Agaoninae of family Agaonidae)

reflects the view that they are a lineage closely related to the major lineages of non-pollinating fig wasps (5 other subfamilies) that are fig parasites¹. In addition to the Agaonidae, several other chalcidoid families include some species associated with figs, and fig-associated lineages varying in size from entire genera to groups of species within genera that are primarily associated with other hosts^{1,59,90}. Historical biogeography of pollinators and other fig wasps does not present clear patterns, for at least three reasons. First, many species remain undescribed; for example, pollinators of many species are unknown. Second, current classifications reflect the uneven intensity of taxonomic research among regions. Recent revisions by Wiebes^{58,89} have led to recognition of a large number of African genera; similar work might well amplify the number of pollinator (and other) genera in other regions. Third, current generic classification probably only poorly reflects phylogenetic relationships. Around nine pollinator genera are found in India⁵³, and they probably represent many of the major lineages. Work on the systematics and biogeography of the pollinators and other fig wasps is urgently required.

Insects from other groups have also become specialized on the diverse fig flora. The biogeography and systematics of many of these sycophilous insects are little investigated in India. For example, in Africa, the radiation of the drosophilid genus *Lissocephala* (whose larvae utilize fig syconia) onto fig species has resulted in numerous drosophilid-fig associations⁹¹⁻⁹⁵. Whether a similar explosive radiation of fig-associated Drosophilidae has occurred in the Asian tropics is unknown, but the richness of both Drosophilidae⁹⁶ and *Ficus*¹⁰ in the Oriental and Australasian regions suggests that similar associations should be looked for⁹⁵. It has been suggested⁹⁷ that the *Lissocephala* of the Orient be placed in another genus. Studies of *Lissocephala* in India might shed light on the origin and niche specialization of this genus.

In some cases, major questions in systematics and biogeography of sycophilous insects could be resolved by studies in India³². The weevil genus *Curculio* is a rare example of a genus of phytophagous insects that has produced a diverse radiation in association with one group of plants in the temperate zone (Fagales of Nearctic and Palaeartic regions), and another diverse radiation with other, unrelated plants in the tropics (Palaeotropical *Ficus* and Myrtales)^{98,99}. The distributions of *Curculio* specialized on Fagales and on *Ficus* meet in north India. The evolution of this unusual pattern of host association might be clarified through comparative studies of *Curculio* in north India. These are but two examples chosen to illustrate the wide range of open questions about the systematics of non-pollinating fig insects that can be examined with systems occurring in India.

Natural history

Natural history of the fig/pollinator mutualism

In this section we present a brief, general discussion of fig natural history. Many of the points discussed are based on studies of only a few species. While many features of basic biology are similar across systems, there exists substantial variation around many themes, and studies of additional species are certain to turn up surprises. We particularly emphasize points where studies of systems occurring in India could greatly advance our knowledge.

The flowers of the fig tree are enclosed in urn-shaped receptacles called syconia. The entrance to each syconium is small opening, bordered by overlapping bracts, called the ostiole. In monoecious fig species (comprising about half of all fig species), each syconium bears a mixture of male flowers and short- and long-styled female flowers. All the syconia on a tree are fairly well synchronized in development. The developmental stages of a syconium are described in detail by Galil and Eisikowitch^{100,101}.

After their initiation, syconia increase in size, eventually reaching receptivity. During this 'flowering' phase, the female flowers inside the syconia become receptive to pollen. Receptive syconia emit one or more volatile chemicals^{102,103} that act as an attractant for the pollinators¹⁰⁴. The pollinators enter the syconium through the ostiole. Once inside the fig, the wasps pollinate the female flowers. However, the wasps can only oviposit in the short-styled flowers; they generally cannot lay eggs in the long-styled flowers because of their length or other features¹⁰⁵. The pollinator usually dies within the fig. During the next few weeks, pollinator larvae develop in the ovules of the short-styled flowers, feeding on ovule contents, and seeds develop in the ovules of the long-styled flowers. After a few weeks, the male flowers in the syconium become mature. At the same time, male and female wasp offspring mature and exit the ovules, and the males inseminate the females. Female wasps then load pollen, either actively or passively, depending upon the pollinator species⁷; both types of pollen loading are represented in Indian genera. The female wasps, bearing pollen, exit the fig through a hole chewed by the male wasps. The wingless male wasps then die; the female wasps fly off in search of other receptive syconia in which to oviposit. Pollinator wasps have a lifespan of only one to three days¹⁰⁶ in which to find a receptive fig. In most studied fig species, individual fig trees flower synchronously and at intervals, so that emerging pollinators do not simply enter receptive syconia on the same tree. The pollinator wasp population is maintained through population-level asynchrony in flowering. At least a few trees releasing wasps and a few trees

receptive to wasps must be present all year round. How such phenologies are maintained in the strongly seasonal monsoon climates that characterize much of India, with marked and often long dry seasons, is an interesting question.

Gynodioecious fig species, comprising around half of all fig species, are found exclusively in the Old World. These species have functionally male and female trees; hence, they are hereafter referred to as dioecious species. The 'male' trees bear syconia containing male and short-styled female flowers, while female trees bear syconia containing only long-styled female flowers¹⁰⁷. Pollinators entering receptive syconia on male trees pollinate and oviposit in the female flowers¹⁰⁸⁻¹¹¹. Male trees therefore produce a mixture of pollen and pollinator wasps on maturation, and no seeds. On the other hand, pollinators entering female syconia pollinate, but cannot oviposit. Hence, female trees produce only seeds. Dioecious fig-pollination systems are paradoxical, because pollination requires that wasps enter female figs, in which they cannot reproduce. The origin and maintenance of such systems pose interesting evolutionary questions¹¹²⁻¹¹⁴, discussed in the next section. India, with representatives of each of the two or three major fig lineages in which dioecy is thought to have evolved independently⁹, is a favoured location for studies of these questions.

Ecology and evolution of non-pollinating fig associates

The fig/pollinator mutualism is the setting for a huge web of interactions with other organisms. Long neglected, the ecology of non-pollinating fig wasps has received more attention recently^{61,90,115-138}. The larvae of these inquilines feed on pollinator wasp larvae within the ovules and/or on ovule contents^{61,138}. In general, these wasps may be characterized as parasites on fig/pollinator mutualisms.

Several other organisms are associated with fig syconia, fig pollinators, or both, and may likewise be considered parasites on the system: yeasts⁹², fungi¹³⁹, nematodes^{140,141}, homopterans¹⁴², mites¹⁴³, dipterans^{91-97,143-147} and coleopterans^{99,121,143,148}. Other insects associated with syconia may have varying effects on fig/pollinator mutualisms. For example, ants may be important predators on pollinators¹²¹, but may also reduce rates of parasitism by non-pollinating fig wasps^{149,150}. Similarly, homopterans may be parasites on the system¹⁴² but also indirect benefactors by attracting ants^{149,150}.

The ecology of fig parasites has received relatively little attention; however, these parasites may influence the evolution of pollinator mutualisms in important ways. In fact, current hypotheses ascribe to insect

parasites a role in selection for closure of the inflorescence in the ancestor of *Ficus*, and thus indirectly a role in the evolution of the fig pollinator symbiosis³¹. Parasites may continue to play a part in the diversification of fig flora in the present. Avoidance of such parasites has also been suggested as a possible advantage of dioecy in figs¹²⁶. Comparisons of the effects of non-pollinating associates on the different reproductive types (monoecious, dioecious and secondarily monoecious) of figs occurring sympatrically in India might yield information on the role played by these associates in the evolution and/or maintenance of fig reproductive types.

The community ecology of non-pollinating fig wasps is particularly amenable to study for two reasons. First, they are specialized on *Ficus* alone, and second, their interactions with the mutualism are quantifiable in terms of pollinators and/or seeds consumed. The communities vary considerably in size; a single monoecious fig species may harbour 10 or more sycophilous wasp species¹⁴³, while a dioecious species may harbour much fewer than ten³². India is a particularly interesting locale in which to study the community ecology of sycophilous wasps because it is possible to study there both the regional variation in communities within fig species, and variation in community ecology among fig species. Studies of niche partitioning among members of the hymenopteran communities^{12,138} may give clues to the evolution of complexity in these parasitic associations.

Many other organisms are indirectly dependent on fig/pollinator mutualisms. Fig species are proposed to be keystone species for frugivores in several forest types because their pattern of year-round flowering and fruiting makes them a continuous food source¹⁵¹⁻¹⁵⁵ (but see Gautier-Hion and Michaloud¹⁵⁶). The frugivores—birds, bats and small vertebrates—serve as seed dispersers, although some are seed predators¹⁵⁷. Insects interact with fig seeds in at least two ways. Lygaeid bugs are seed predators^{121,158-160}. Ants secondarily disperse seeds of *F. microcarpa*, an Indian species introduced to Florida¹⁶¹. It would be interesting to see the degree to which ant dispersal occurs in native settings, and to study possible adaptations of figs to dispersal by ants.

Coevolution of plants and insects

Co-cladogenesis or host transfers?

With species specificity and the existence of ca. 750 fig/pollinator pairs, figs and their pollinators offer rich material for the study of coevolution, a focus of much recent work on insect/plant interactions¹⁶². Cladograms depicting relationships of different sections of the

genus *Ficus* match reasonably well with those of genera of the agaonid pollinators^{7,53}, suggesting co-cladogenesis. However, many uncertainties remain. First, and most importantly, phylogenetic relationships for both figs and their pollinators are very uncertain at higher taxonomic levels⁵³. The morphological characters used in wasp taxonomy are arguably related to adaptation to fig hosts, and some similarities may be due to convergence, rather than to shared ancestry. The same problems exist for fig taxonomy. Additional characters whose evolution is not constrained by the mutualism must be used. Second, within the matches between groups of related figs and groups of related wasps, there are incongruencies that may indicate host shifts. The pollinators of species of section *Conosycea*, for example, belong to five genera and almost certainly represent more than one independent radiation onto this section⁷. Third, even when related figs tend to have related pollinators, and phylogenies are congruent, there exist alternatives to the hypothesis of co-cladogenesis¹⁶³. Based on current evidence, both co-cladogenesis and host shifts seem to have played roles in the radiations of figs and their pollinators, but the exact contribution of each remains uncertain. The phylogenies of figs and pollinators are currently under revision^{9,89}; the results should yield interesting material for research on parallel evolutionary radiation.

Speciation and host shifts

If host shifts have played a role in diversification of figs and their pollinators, as phylogenetic patterns suggest, several types of questions may be posed. How have host shifts led to speciation? Discussion of this complex question is beyond the scope of this review. Many features of the biology of fig pollinators (host specificity; mating occurring on the host plant, and prior to dispersal; high rates of inbreeding) suggest that speciation via host race formation¹⁶⁴ may be rather easy in this group.

How can the specificity so characteristic of fig/pollinator relationships break down sufficiently to allow host shifts? Studies of several kinds are providing information on this question. First, exceptions to one-to-one specificity of fig and pollinator species occur in nature, and studies suggest that host shifts may account for some of these. Second, species introductions, and possibly extinctions, constitute 'natural experiments' that provide opportunities for studying mistakes. Third, fig/pollinator associations can be manipulated in controlled experiments, to test the consequences of specificity breakdown.

Exceptions to one-to-one specificity in nature. A single fig species may be associated with two (or more)

pollinator species that coexist sympatrically⁴ or occur in different parts of the plant's geographic range⁶. Conversely, a single pollinator species may be associated with two or more fig species⁷. Indian systems offer no documented examples of such exceptions to one-to-one specificity in nature. Some suggestive cases are probably taxonomic artefacts, disappearing, for example, when new synonymies are established (see examples for *Eupristina* in Wiebes⁵⁶). Still, based on results from recent African studies, good examples may yet be discovered in India. Existing literature offers suggestions on where to look. *Eupristina verticillata* is the pollinator of *F. microcarpa*, but *E. saundersi* (from a different subgenus than *E. verticillata*) was listed for this fig species in an old record from West Bengal that Wiebes^{13,56} considers questionable. Other suggestive examples concern cases where an unusual pollinator is recorded from another part of the geographic range of a fig species that occurs in India. For example, the usual pollinator of *F. benjamina*, in India and elsewhere, is *Eupristina koningsbergeri*, but *E. emeryi*, from a different subgenus, is recorded from this species in Papua New Guinea and Java⁵⁶. In similar fashion, wasp species associated with one fig species in India may pollinate other fig species elsewhere. For example, the pollinator *Kradibia gestroi* is reported from three fig species (*F. exasperata* in India, this species plus *F. asperifolia* and *F. capraefolia* in Africa), each from a different series of section *Scyidium*, subsection *Varinga*⁷. Further work in India may resolve existing uncertainties, uncover good examples of exceptions to specificity, and clarify whether such examples are due to host shifts or to other processes.

'Natural experiments'. Species introductions facilitate the study of 'mistakes' for two reasons. First, 'mistakes' may occur at a low frequency in nature, but this 'background noise' is much more easily detectable when the usual pollinator of a species is absent. When a fig species is introduced without its pollinator into an area containing other fig/pollinator systems, the only pollinated syconia are those that result from mistakes^{6,166}. Second, introductions may increase the frequency of mistakes. The main proximate mechanism maintaining specificity is the host-orienting behaviour of the female wasps. If behavioural specificity can be overcome, we can examine what happens when 'mistakes' occur. Species introductions constitute a sort of uncontrolled natural experiment, producing novel sympatric combinations of fig and pollinator species. Avoidance of 'wrong' figs is a character shaped by selection, and when figs or wasps are confronted with associates beyond their evolutionary experience, specificity may break down^{143,167}. Also, when figs are unpollinated, they remain receptive and attractive for up to several weeks; an unpollinated tree of an

introduced species may thus accumulate a large crop of receptive figs. The large number of unvisited figs, receptive for an unusually long period, may trigger an unusual number of 'mistakes'¹⁶⁸.

One such group of natural experiments involves Indian figs, and some of their pollinators, introduced into subtropical south Florida¹⁶⁹. Both *F. altissima* and its pollinator, *Eupristina altissima*, are established there. In addition to its normal host, *E. altissima* also enters figs of *F. religiosa*, *F. benjamina*, and *F. drupacea*, three species whose pollinators are absent. Success of pollination and of wasp development varies in a fashion correlated with phylogenetic distance of the novel host from the normal host¹⁷⁰. This case involves fig species whose natural ranges in India overlap¹⁰; it is possible that the 'mistakes' observed in Florida also occur in natural settings, but have gone undetected.

Another type of natural experiment may result when a population of figs is reduced to a number of individuals insufficient to maintain the pollinator population (see next section). In such cases, will the fig be at least occasionally visited by pollinators of other, sympatric fig species? Situations in which fig populations drop below critical population size, thankfully still hypothetical, should be watched for in the increasingly fragmented, fig-rich forests of areas such as the Western Ghats.

Experimental manipulation of host associations. In addition to natural experiments resulting from species introductions and local extinctions, planned and controlled experiments can be conducted in which wasps can be induced to enter 'wrong' figs, even sympatrically occurring species they normally avoid. These 'mistakes' can be induced by placing recently emerged pollinators, highly motivated to search for receptive figs, directly on the ostiole of receptive figs of an inappropriate species¹⁷¹.

Such experiments permit estimation of the fitness consequences of mistakes. Results from such experiments so far suggest that host shifts are relatively easy. Wasp fitness in a novel host is reduced relative to that in the usual host, but is greater than zero¹⁷⁰⁻¹⁷². Combined with experiments to determine the chemical-ecological basis of wasp attraction and specificity¹⁰⁴, they provide insight into what kinds of host shifts may be most likely to occur, offering means of investigating several important questions: (i) What factors influence the likelihood of a breakdown in specificity? For example, does seasonal shortage of syconia of the appropriate host increase the probability of mistakes? (ii) What factors influence the kinds of mistakes that are made? Do related fig species possess similar volatile attractants? (iii) What factors influence the probability that a mistake will result in at least limited success? Is successful development of wasp and seeds more likely

when mistakes match close relatives of the normal associates? If host shifts are more likely to involve closely related hosts and closely related pollinators, then very detailed studies may be necessary to distinguish between the alternative processes of co-cladogenesis and host shifts in the diversification of fig/pollinator mutualisms. India, with its rich diversity of fig/pollinator systems that include series of closely related species as well as representatives from widely separated lineages within both *Ficus* and pollinating fig wasps, offers great scope for such studies.

Maintenance of the mutualism: Critical population size, seasonality and fragmented forests

The short-lived pollinators of figs can be maintained in fig populations only through a more or less continuous flowering throughout the year. If the population consists of a limited number of fig trees, there may be instances in which wasps released from a tree find no receptive figs (resulting in male failure), or in which no tree releases wasps during the period when a tree is receptive (resulting in total failure of the crop). If either male failure or total failure occurs at the population level, the wasp population goes extinct. Hence, a minimum population size of fig trees (termed critical population size, or CPS¹⁷³) is required to maintain a wasp population over the long term.

Seasonal environments may favour seasonality in flowering and fruiting, and in fact, in seasonal environments in south Florida and on Barro Colorado Island in Panama, fig trees produce low numbers of syconia at certain times of the year¹⁷⁴⁻¹⁷⁶. CPS in seasonal environments should be affected by the requirement to maintain pollinators during seasonal troughs in flowering activity. Simulation models confirm the intuitive supposition that seasonality should increase CPS^{15,177}.

Indian fig/pollinator systems, subjected to strongly seasonal climates, offer many opportunities for testing hypotheses about the effects of seasonality on the functioning of these mutualisms. The monsoonal climate of India, combined with the sharp precipitation clines created by mountain ranges such as the Western Ghats and the Himalayas in turn create a variety of habitats, varying in degree and pattern of seasonality, within relatively short distances. Hence, field studies in sharply contrasting environments are feasible, and would enable one to distinguish between phenotypic plasticity and genetic adaptation in the phenological responses of figs to seasonality.

Extinction of pollinator populations (and thus of fig populations as well) is the most extreme effect of seasonality on fitness of figs and wasps. Even at populations above CPS, however, models predict occasional

male failure and total failure of crops, and seasonality increases their incidence^{15,177}. The resulting reduction of fig or of wasp fitness may select in each species for adaptations that reduce the negative effects of seasonality. Janzen¹⁷⁸ suggested that a seasonal breakdown in within-tree flowering synchrony might allow pollinators to re-enter flowering syconia on their natal tree during harsh seasons, and to shelter within these trees until the main flowering season. The cost to the tree of wasted reproductive function might be offset by the benefits of maintaining a pollinator population that could pollinate other trees when syconia became abundant¹⁷⁸. In fact, studies show that within-tree asynchrony that allows wasp transfers within the same tree is rare¹⁷⁴, and that within-tree asynchrony occurs least frequently during harsh seasons^{120,174,179}.

Bronstein¹⁴ and Bronstein *et al.*¹⁷³ have suggested two other traits that might allow fig and pollinator populations to survive in strongly seasonal environments. First, fig wasps may evolve increased lifespan or flight capability. Second, plasticity of syconial development time may enable wasps to remain inside syconia for longer periods during harsher seasons¹⁸⁰. In addition, simulation models and field tests suggest that increased duration of receptivity may greatly reduce the number of fig trees necessary to maintain a pollinator population^{177,181}. All these hypotheses require further testing, and comparative studies of Indian systems in environments of varying seasonality offer conspicuous opportunities for such tests.

In fig/pollinator mutualisms already constrained by seasonality, fragmentation of fig populations due to human activities poses an additional threat. Is forest reduction and fragmentation reducing populations of fig species to numbers perilously close to CPS, or even below it? Remaining forest is being rapidly removed or degraded, and areas such as the Western Ghats and lower Himalayas are considered among the world's extinction hotspots¹⁸². Predicting the effects of human activities on the stability of fig/pollinator mutualisms requires many types of information. (i) What is the CPS of fig populations? Computer simulation models show that for certain parameters of wasp and monoecious fig ecology, a median of 95 trees is required to maintain pollinator populations for a four-year period¹⁷³. The number may be much higher when a longer timeframe is considered¹⁶⁹. CPS is sensitive to many parameters, and estimates of CPS for particular empirical situations are lacking. (ii) What are the densities and sizes of fig populations? Does forest conversion translate to fig population reduction, or do figs persist or become more abundant in secondary growth? If figs are restricted to patches of relatively undisturbed forest, do these increasingly insular patches contain enough figs to maintain populations of their respective pollinators? The conservation of sacred groves is particularly important¹⁸³,

because fig trees, considered sacred, might occur in such forests at densities sufficient to maintain pollinator populations.

Knowledge of the effects of human activities on stability of fig/pollinator mutualisms may have far-reaching implications for conservation biology. By ensuring that a minimum number (the CPS) of fig trees is included within an area to be protected, scientists and administrators would ensure the survival of the animal, bird and insect communities that depend upon these keystone species¹⁶⁹.

The evolution and maintenance of dioecy

Seasonality and the evolution of dioecy

Kjellberg and Maurice¹⁵ suggest that in seasonal environments, the relative value of male and female functions might be increased at different times of year, selecting for peaks in wasp and seed production during those times of year. Such sex allocation might be relatively easy to achieve through alteration in style length, which determines whether wasps or seeds will be produced. Strongly seasonal climates might lead to the formation of two phenotypes, one male and one female, that display seasonal peaks in flowering, with male phenotypes flowering synchronously and delivering pollen to synchronously flowering female phenotypes.

The scenario envisioned above by Kjellberg and Maurice¹⁵ leads to three predictions: (i) dioecious figs will possess phenologies in which male trees flower in a peak and deliver pollen to synchronously flowering female trees, and maintain pollinators within trees by a low level of flowering during the rest of the year; (ii) that dioecious fig species perform better in some important sense (i.e., are more fecund, possibly even more abundant) in seasonal than in aseasonal environments; and (iii) that in monoecious species, one might find within-tree or among-tree changes in allocation to male and female function in seasonal environments compared to less seasonal ones¹⁵. India's distinctly seasonal climate and the co-occurrence of monoecious and dioecious species in many forests makes it possible to test all of the above hypotheses.

The first prediction mentioned above was based on the phenology of *F. carica* in France¹¹³. Research on another dioecious fig species, *F. exasperata* in India¹⁸⁴, indicates that the phenology and distribution of this species tend to fit the first and second predictions. *Ficus carica* and *F. exasperata* are members of two evolutionary lineages representing two different pathways to dioecy³¹. Hence, dioecy may have evolved in a seasonal environment in at least two lineages of *Ficus*.

Dioecy in aseasonal environments

The discussion above implies that dioecy in figs evolved

in seasonal environments, and that dioecious figs may be expected to be more abundant in such environments. However, one section of dioecious figs, section *Sycocarpus*, is centred in parts of the Oriental and Australasian regions that are characterized by a relatively aseasonal climate. The phenologies of two species in this section, *F. hispida*¹⁸⁴ and *F. fistulosa*¹⁸⁵, are distinctly aseasonal, characterized by year-round flowering. In addition, *F. hispida* tends to be more abundant in a wetter, less seasonal environment than in a more seasonal one¹⁸⁴. If this pattern is confirmed in most species of section *Sycocarpus* (and in its likely sister group, section *Adenosperma*), it may indicate that dioecy in this section has evolved in a relatively aseasonal environment. Whatever the environment in which dioecy originated in this lineage of figs, it is clear that dioecy can be maintained in aseasonal environments. India possesses seasonal and relatively aseasonal environments which contain elements of different evolutionary lineages of dioecious figs occurring sympatrically. Comparative phenological studies might reveal how dioecy evolved in different lineages, and how that affected their eventual biogeographic distribution.

The possibility of at least two different paths to dioecy in *Ficus* implies that we must search for other hypotheses that might explain the evolution of dioecy in seasonal and aseasonal environments alike¹⁸⁶. For example, the advantages of differential resource allocation toward male and female function might prove to be a significant factor in the evolution of dioecy in all environments. Selection pressures on the morphology and phenology of male syconia are different from those on female syconia. Female syconia, freed from the developmental time imposed by the pollinator³¹, may evolve a number of adaptive traits that require longer maturation times, such as fleshier fruit¹⁸⁷. Also, female trees are freed from the constraint of spacing crops to prevent wasps from entering their natal tree; therefore, they may be able to flower continuously, obtaining large numbers of pollen donors, and fruit continuously, sampling a large variety of environments in space and time¹⁸⁷. Studies of *F. hispida* and *F. exasperata*, two dioecious figs in India, have shown that both species possess sexual differences in syconium morphology and developmental time and in individual tree phenology that are advantageous in both seasonal and less seasonal environments¹⁸⁴. Future studies of sexual differences in morphology and/or phenology among various dioecious figs species would help in determining other advantages of (and possible paths to) dioecy in various environments. Because the phenologies of two Indian dioecious fig species are now relatively well-known¹⁸⁴, the foundation for more detailed studies has already been laid in India.

Evolutionary stability of the dioecious fig-pollinator system

There appear to be strongly opposed selective forces acting on wasps and dioecious fig species to destabilize the dioecious fig/pollinator system. Individual wasps that enter receptive syconia on female fig trees cannot lay any eggs, and their fitness is zero, whereas those that enter syconia on male trees have non-zero fitness, because they usually leave offspring. There should be strong selective pressure on pollinators to avoid entering female figs^{112,113}. Such selection could occur rapidly because the generation time of pollinators (a few weeks) is much shorter than that of figs¹¹³. Why then do dioecious figs still exist? Their phenology may provide one mechanism for their persistence. In some dioecious fig species, (*F. carica*, *F. exasperata*), male and female syconia almost never flower simultaneously; because wasps exiting male trees either enter female trees or die, selective pressure on wasp choice is effectively neutral¹¹³. However, in other dioecious species (*F. hispida*, *F. fistulosa*), male and female trees frequently produce receptive syconia simultaneously. In such species, selection for wasp choice should exist.

Patel *et al.*¹¹⁴ designed an experiment in the wild to present fig pollinators exiting a male tree with a choice between receptive male and female syconia. The results of the experiment indicate that wasps do not choose receptive syconia based on sex. We hypothesize that several factors might combine to prevent wasp choice from evolving¹¹⁴. Further research on the physical and chemical basis of wasp attraction, studied across sexes, is required to determine how the dioecious fig/pollinator mutualism remains extant. The known phenologies of two dioecious species in India¹⁸⁴ make it possible to formulate and test different hypotheses on wasp attraction to male and female figs.

Finally, destabilizing forces acting on dioecious fig/pollinator mutualisms may account for the evolutionary reversion to monoecy that seems to have occurred in subgenus *Sycomorus*. Studies of the widespread Indian representative, *F. racemosa*, may suggest hypotheses to explain how secondary monoecy might have evolved.

Ethological aspects of fig-pollinator interactions

This review has been written primarily from a plant-centred perspective, reflecting the backgrounds of its authors. However, many of the topics discussed have an important ethological component. These include the natural history of fig pollination^{3,83,108,109,188}, relationships between the mutualists and parasites on the system, mechanisms maintaining host specificity, traits that permit host shifts, the analysis of conflicts between

fig and wasp reproduction, and the origin and evolutionary stability of dioecy. In all these areas, interactions between figs and fig insects raise many questions for ethologists, questions that could hardly be adequately reviewed here. We briefly present selected examples, to illustrate some potential contributions of ethology to the study of these systems. (i) Why and how has the behaviour of active pollination¹⁸⁸, virtually unique to the fig-pollination system, evolved apparently several times from passive pollination^{53,189}? What is the advantage of active pollination to the wasps? Studies of a small number of species support the contention that fertilization of ovules is necessary to ensure successful development of pollinator wasp larvae¹⁹⁰. Is this generally true, for passively as well as for actively pollinated species? What is the plant's evolutionary response to the evolution of active pollination? With more efficient pollen transfer, do actively pollinated fig species reduce their investment in pollen production¹⁹¹? (ii) What is the role of wasp behaviour in determining the relative numbers of seeds and wasps produced in monoecious figs¹⁰⁵? (iii) How does a female wasp regulate the sex ratio of her offspring¹⁹²? Can a female assess her genetic relatedness to other foundresses within the same fig, and modify the sex ratio of her offspring accordingly¹⁹³? (iv) What are the proximate mechanisms maintaining pollinator host-specificity? Studies of volatile attractants of figs¹⁰⁴ lead to a host of interesting questions about the neuroethology of wasp responses to host-plant chemistry. (v) How are dioecious fig pollination systems maintained? Ethologists can make essential contributions to understanding the evolutionary stability of these systems, and to explaining how some dioecious systems have reverted to monoecy^{194,195}.

Conclusion

Fig-pollinator interactions pose important and interesting questions for naturalists, systematists, biogeographers, ecologists ethologists, and evolutionary geneticists. In addition to providing engaging questions for biologists from numerous disciplines, fig-pollination systems provide an excellent focus for the application of different and complementary approaches (e.g., modelling and empirical studies) to the study of evolutionary problems. They also offer great opportunities for applying modern evolutionary biology to the urgent problems of conservation.

India's biogeographic location, its diversity of fig flora, and its strongly seasonal climate make it an ideal location to study several as yet unanswered questions regarding the fig/pollinator mutualism. In addition, India possesses good laboratory and communications facilities that are relatively close to potential field sites;

hence, projects involving both field and laboratory work may be accomplished relatively easily. Finally, researching the fig/pollinator mutualism is a low budget and high reward activity—any biologist's dream! We therefore hope that this review will spark a renaissance of fig research in India.

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Coevolution of plants and animals: Pollination of flowers by primates in Madagascar

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Observations on the floral biology of the traveller's tree (*Ravenala madagascariensis*) and the ecology of the ruffed lemur (*Varecia variegata*), both endemic to the island of Madagascar, suggest a closely coevolved plant-pollinator relationship. The plant has many specializations for flower visitation by large non-flying animals and the lemurs appear to be dependent on nectar as a food source during specific times of the year. The basal phylogenetic position of *Ravenala* in the family Strelitziaceae, which diversified in the late Cretaceous and early Tertiary, is consistent with the hypothesis that pollination by lemurs is an archaic system in the family whereas bird- and bat-pollination systems are derived in the more advanced genera. These results provide supporting data for earlier hypotheses on the evolution of non-flying mammals as ancient pollinators of flowering plants.

THE origin and explosive diversification of flowering plants during the Cretaceous is often attributed to the simultaneous radiation of insects, which served as

critical pollen-dispersal agents¹. Vertebrates are thought to have played a negligible role in the early evolution of angiosperms because the main groups, which are important pollinators of extant plant taxa (e.g. birds and bats), originated no earlier than the Eocene^{2,3}. However, non-flying mammals, such as marsupials and primates which are known nectar feeders, appeared as early as the middle Cretaceous and Paleocene³⁻⁵. Sussman and Raven⁴ have suggested that these non-flying mammals could have been significant pollinators since the uppermost Cretaceous, but were outcompeted in the Tertiary by nectar-feeding birds and bats. Any coevolved relationships between flowering plant species and non-flying mammal pollinators that persist at the present would appear to be "... "living fossils", which have a great deal to tell us about the evolution of both the mammals, including some of our own antecedents, and of the flowering plants"⁴.

Many non-flying mammals, such as rodents⁶, genets⁶, tree shrews⁷, procyonids⁸, marsupials⁹, primates⁸⁻¹³, and even giraffes¹⁴ feed on nectar or flowers. Among