

## Multi-author Review

### The comparative biology of figs

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#### The fig/pollinator mutualism: A model system for comparative biology

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#### *The ways to be a fig*

Coevolution, the reciprocal evolutionary response of one species to another<sup>2</sup>, has attracted wide attention during the last twenty-five years. Nevertheless, it remains difficult for biologists to document. Recent work has shifted to identifying forces that may often *prevent* coevolution, such as variability in the relative and absolute effects of associations with different partners over time<sup>5, 7, 11, 13</sup>. But some well-documented examples do exist and tend to be cited repeatedly in treatments of coevolution. These include the spectacular example of the fig/pollinator mutualism. Its extreme species-specificity, in particular, has led this interaction to be considered as a 'limiting case' of what coevolution can produce, and has provided a cornerstone against which other interactions are compared. However, this superficial view has probably hampered understanding of the fig/pollinator mutualism. It is increasingly apparent that 'the' interaction is a fiction: there are in fact over 700 independently interacting pairs of figs and pollinators. In its usual, abstract form, it can reveal little about processes and consequences of coevolution. But such enormous diversity offers the much more exciting possibility of separating those features of a coevolved interaction that are highly canalized and constrained, those that have responded to identifiable selection pressures, and those that are more plastic. Moreover, that diversity allows the many *consequences* of coevolution (limits to species' distributions, relationships with associates such as seed dispersers, etc.) to be approached. Understanding these coevolutionary consequences should, in turn, lead to a deeper appreciation of the critical roles figs play within forest communities, with important implications for conservation decisions in the tropics.

Not surprisingly, the comparative biology of the fig/pollinator interaction is now attracting attention from a wide spectrum of biologists. This interest generated an

NSF/CNRS research colloquium in Miami in 1988, and has provided the basis for this multi-author review. We believe that it will become clear to the reader that the broad implications of these comparative studies well justify the amount of attention being paid to such a specialized plant genus and the hymenopteran family associated exclusively with it.

#### *Natural history*

As background, we first provide an overview of the fig pollination mutualism. (Further details are provided in the contributions of Verkerke and Bronstein.) Figs (*Ficus* spp., Moraceae) can only be pollinated by female agaonid wasps (Hymenoptera: Chalcidoidea: Agaonidae); the wasps in turn can only lay eggs within *Ficus* inflorescences (syconia), wherein their offspring feed on some of the developing seeds. Species of fig are nearly always associated with a single species of agaonid wasp.

Roughly half of the 700 *Ficus* species are monoecious, and half gynodioecious. The pollination biology of the monoecious species, which include all New World representatives, is much better understood. Typically, large numbers of pollen-carrying female wasps arrive at a fig tree when it is bearing thousands of synchronously initiated syconia. Each is a hollow multiple receptacle lined with several hundred male and female florets. At the time the wasps arrive, only the female florets are receptive. The wasps enter the syconia via the ostiole, a bract-covered pore. Once inside they deposit pollen on the stigmas, then oviposit directly into some of the ovaries via the styles. However, because style length is highly variable, the ovaries vary in accessibility to the wasps. This (among other, less studied factors) guarantees that a mixture of seeds and seed-eating wasp offspring matures within each syconium. After several weeks, the

males emerge, locate the females, and inseminate them. Females then emerge and collect pollen from the newly mature anthers, while males tunnel out through the sealed wall of the syconium. The females then depart in search of other syconia in which to oviposit. As a rule, syconia on an individual tree are highly synchronized, whereas different trees flower out of synchrony. Therefore, departing wasps must locate another tree in the correct sexual phase.

In the remaining fig species, trees either bear syconia with both female and male florets, or with female florets only. When wasps enter syconia on the hermaphroditic trees, they can oviposit in every female floret because the styles are uniformly short. These trees successfully rear the pollinators' offspring, but few or no seeds, and therefore function as pollen donors. If the wasps enter syconia on female trees they encounter only long-styled florets. Although they deposit their pollen load they cannot oviposit, and these trees consequently are seed producers only. Hence these species are gynodioecious, but functionally dioecious.

#### *A model system for comparative biology*

As Frank points out in his contribution, three papers published in 1979 were influential in directing biologists' attention to the central ecological and evolutionary questions posed by this unusual natural history story. Wiebes<sup>15</sup> summarized fig and pollinator phylogenies and discussed what they might reveal about processes of co-evolution and cospeciation. Janzen<sup>8</sup> and Hamilton<sup>4</sup> reviewed ecological features of the interaction and considered the evolutionary processes that may have led to them. These studies raised many more questions than they answered. In fact most of these questions have yet to be answered (although one of us has had a paper rejected on the grounds that 'everything interesting about figs was said by Janzen in 1979'). Along with earlier classics (e.g. <sup>3,6,10</sup>), these three papers have stimulated a new generation of biologists to study this mutualism. Many of us, independently, have discovered the value of using the comparative approach to do so.

The great scope that fig/pollinator systems offer for testing hypotheses with comparative methods is, paradoxically, a consequence of their highly stereotyped nature. Much of the interaction occurs in a restricted microhabitat (the syconium) that is stereotyped ecologically across species. Because that microhabitat comprises the most significant portion of the environment for the wasps, cross-species comparisons (at least of the wasps) are less likely to be muddled by environmental differences extrinsic to the interaction. Of course, those features that are also stereotyped evolutionarily (that is, shared among all species by common descent) cannot be studied by comparative methods. For example, all agaonid wasps mate within the syconium, and males are wingless in every case. Yet other, related features have evidently evolved

independently several times; for instance, agaonid sex ratios vary greatly and correlate with syconium dimensions (see Herre's contribution). Hypotheses about the evolutionary significance of these traits posed from work with one lineage can be tested by examining other lineages, provided that reliable information is available about phylogenies. The possibility of such extensive replication at this fine taxonomic scale is rare in comparative biology.

Comparisons within species are possible as well. Among-site comparisons can be particularly informative. Over the range of a given fig species, the stereotyped pollination interaction may take place in widely divergent environments, offering the opportunity to study selection pressures and their consequences. For example, flowering is difficult at some times of year at the margins of figs' tropical range. Short-term consequences include lowered pollinator survivorship and thus lowered fig reproductive success as well; longer-term consequences may include selection for a breakdown in within-individual flowering synchrony at those sites and even sexual specialization among trees (discussed in the contributions of Bronstein, Windsor et al; and Kjellberg and Maurice). Comparisons among individuals at a single site can also be drawn. For example, Bronstein examines levels of crop asynchrony within fig populations to test an hypothesis about the adaptive value of this trait in seasonal sites. Kjellberg and Maurice use simulation models to compare theoretically the performance of different flowering strategies in such environments.

It should be clear that a variety of comparative approaches can and should be taken to the same study system. Frank points out that within-species comparisons ideally feed back to generate hypotheses about among-species differences. We hope more generally that new ideas will be raised by reading these very different papers in juxtaposition.

#### *Scope of this review*

The bedrock of all comparative studies in ecology and evolution is a good knowledge of evolutionary relationships within the study system. Phylogenies of figs and pollinators have been studied in depth for many years (reviewed in Wiebes<sup>14</sup>), notably by J. T. Wiebes (Agaonidae) and E. J. H. Corner (*Ficus*). Due to the size of the taxa and scarcity of informative characters, most of the work remains to be done, particularly at the fine scale; in fact perhaps half of all agaonid species have yet to be identified. Thus, for example, it may still be too early to test hypotheses about cospeciation of the mutualists<sup>1,16</sup>. However, the main subdivisions of *Ficus* and Agaonidae are relatively well worked out. They are presented here by C. C. Berg, the prominent authority on *Ficus* today. All of the subsequent contributions depend explicitly or implicitly on the systematic studies that Berg synthesizes. For example, hypotheses for the derivation

and adaptive significance of gynodioecy in *Ficus* (see Verkerke, Bronstein, and Kjellberg and Maurice) originate from systematists' conclusions about its taxonomic and biogeographic distribution.

Many of the most important structures used for classification in *Ficus* are syconium features that happen to be critical during ecological interactions with their pollinators. A link between systematics and ecology within this study system is provided in Wouter Verkerke's contribution on the functional anatomy of the syconium. Verkerke describes the structure of this unique inflorescence, details how it varies among the sections of *Ficus* and with breeding system, and suggests the possible functional significance of that variation for the pollination interaction. He also summarizes his pathbreaking work on the ontogeny of different flower types and of the syconium as a whole. This work is providing the most comprehensive picture yet of the origin and development of fig traits critical to the dynamics of the pollination mutualism.

The coevolutionary dynamics of this mutualism, however, are set by an interaction between these traits and traits of the agaonid wasps. E. Allen Herre concludes from his comprehensive studies in Panama that a complex interplay between fig flower number and pollinator sizes and numbers affects reproductive success of both partners. Moreover, he shows that the evolutionary interests of the mutualists often conflict, in the sense that traits maximizing success of one species apparently diminish the success of its partner. Herre's conclusions are of major significance for understanding the evolution of mutualisms. His work provides a textbook example of how ecological comparisons among closely related species at a single site can generate evidence for evolutionary processes.

Judith Bronstein's contribution serves to point out that not only the enclosed environment of the syconium, but also the external environment affects the ecology and evolution of this mutualism. Fig and pollinator success closely depend on the ability of the minute wasps to locate flowering trees. Bronstein's conceptual models indicate that flowering frequency and flight conditions are thus both critical, and should depend critically on climate. She examines the evolutionary consequences of these constraints by contrasting fig traits (particularly aspects of flowering phenology) both among populations at different latitudes, and within populations during different seasons. Her use of the comparative approach leads her to question two adaptive scenarios explaining how figs can persist at the edge of their range, and to pose alternative hypotheses.

Bronstein and other contributors stress that the evenness of flowering through the year within a fig population should be of central importance to the success of the pollination interaction. Empirical data on fig phenology are, however, very scanty. Studies of two Panamanian species published by Milton et al. in 1982<sup>9</sup> provided the first good evidence that in seasonal habitats, seasonal

rhythms are imposed onto population-level flowering phenologies. Donald Windsor and collaborators now extend that conclusion by presenting multi-year phenologies for six other fig species at the same site. His data allow us to separate for the first time aspects of flowering and leafing phenology that are specific to individuals, common within species, and common among species at one site. In combination, the work of Windsor, Herre and their collaborators have made the fig community of Panama's Barro Colorado Island by far the best understood in the neotropics.

The models of Finn Kjellberg and Sandrine Maurice examine how seasonal flowering rhythms such as those described by Windsor et al. might become established, and what their consequences might be. Using comparisons of reproductive success among individuals within their simulated populations, Kjellberg and Maurice show that when conditions vary seasonally, phenotypes with different flowering times should succeed differentially via the female (seed-producing) and male (pollen-donating) functions. Highly seasonal conditions could therefore lead to the evolution of sexual specialization in *Ficus*. While the time scale they consider is one that could only be studied with a theoretical approach, Kjellberg and Maurice generate a number of hypotheses that should be testable by comparative field studies.

Kjellberg and Maurice's models are based on the concept of a 'critical population size' for figs: since pollen-carrying wasps departing from one tree must immediately locate another tree in the opposite sexual phase or else die, some minimum number of trees is required to sustain a local pollinator population over time. Without a pollinator population, the figs cannot reproduce. Doyle McKey discusses the ecological consequences of this phenomenon, as well as its practical implications for conservation. For example, critical population size provides a major constraint to range extensions of each partner: pollinators arriving at small fig populations at the range margin will be unable to persist, limiting seed production and consequently the spread of fig trees. In this context, McKey examines some intriguing instances in which the pollinators of ornamental *Ficus* species have unexpectedly arrived and become established far from their native habitats. (Some of these figs now show signs of becoming part of the pantropical weed flora). One direct consequence of maintaining pollinators within a fig population is that fruiting, not only pollination, will occur successfully year-round. This means that figs may often be 'keystone resources'<sup>12</sup> for frugivorous mammals and birds, supplying food during periods when little else is available. Possibly no other plant genus has as large a role to play in the maintenance of local diversity in tropical forests. Thus, McKey emphasizes that concerns about population sizes in this system are not strictly academic. Finally, Steven Frank's contribution reviews the status of five key topics in fig research and identifies many of the central questions that should occupy students of this

system in future years. Three of these topics relate directly to the mutualism, and here Frank's discussion provides an overview of the other papers in this symposium: limits to seed versus agaonid production within syconia, flowering phenology and its consequences for wasp population dynamics, and monoecy versus dioecy. The other two subjects – parasite pressure and wasp behavior – are not yet well investigated, but can be predicted to have major consequences for the fig/pollinator interaction. Frank conceptualizes this system with three kinds of contrasts. First, he discusses the evolutionary versus ecological dynamics of species interactions, and indicates how ecological studies can generate hypotheses about evolution. Secondly, he contrasts developmental and selective processes that may contribute to producing an observed ecological pattern. Lastly, he compares within-species and among-species patterns and what each might reveal about the other. Throughout, Frank emphasizes the need for good phylogenies before initiating comparative studies. Thus, our final contribution provides a conceptual link back to the first.

#### Conclusion: Broader implications of fig studies

Even if current rates of worldwide deforestation were to stabilize, it is increasingly clear that biologists will not have time to study most tropical interspecific interactions before they disappear. Consequently, some conservationists have suggested that it may be most fruitful to identify and concentrate attention on a few important systems that have the potential to be understood in depth.

We suggest that fig/pollinator mutualisms are prime candidates for such 'salvage ecology'. First, large numbers of species are involved, with representatives probably found in most tropical habitats worldwide. Secondly, as we have emphasized previously, each interaction has been a 'laboratory' of coevolution; comparative studies within and among species provide an ideal tool to dissect poorly understood coevolutionary processes and the patterns they produce. Third, these appear to be keystone mutualisms, that is, interactions upon which other species depend and around which they accumulate. Thus, ecological studies and conservation efforts focusing on figs will inevitably shed light on the communities in which they occur.

Finally, this multi-author review documents that a good start has already been made towards understanding the diversity, biogeography, coevolutionary processes, and community consequences of fig/pollinator mutualisms. We wish to emphasize, however, that most aspects remain to be studied. For instance, what explains the explosive speciation that has occurred among figs and their pollinators? How is the extreme species-specificity of the interaction maintained? How have sex allocation patterns evolved within fig species, and within pollinator species? How important are figs in regulating the num-

bers of frugivorous animals in tropical forests? Efforts to answer these questions must race against increasing rates of habitat degradation.

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