

Evolutionary Ecology of Figs and Their Associates: Recent Progress and Outstanding Puzzles

Edward Allen Herre,¹ K. Charlotte Jandér,^{1,2}
and Carlos Alberto Machado³

¹Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama; email: HERREA@si.edu

²Department of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853

³Department of Biology, University of Maryland, College Park, Maryland 20742

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Abstract

Over the past decade a proliferation of research has enriched and dramatically altered our understanding of the biology of figs, their pollinator wasps, and the myriad of other organisms that depend on them. Ecologically, this work underscores the crucial role that fig fruits play in sustaining and shaping tropical frugivore communities. More generally, this work addresses several key issues in evolutionary ecology, including evolution of breeding systems (shifts between monoecy and dioecy), factors that promote the stability of mutualisms, precision of adaptation, and trajectories of community assembly and coevolution in systems with multiple interacting partners. Moreover, both the pollinating and nonpollinating wasps associated with figs provide unparalleled opportunities for examining how different population structures can differentially affect sex allocation, kin selection, the evolution of parasite virulence, and many fundamental parameters of population genetics (e.g., levels of genetic variation and rates of silent and nonsilent base substitutions).

"If you study tropical frugivores, or carnivores for that matter, directly or indirectly you will end up studying figs."
-Charles Handley, Curator of Birds and Mammals, National Museum of Natural History, Washington, DC, 1950–2000

"If you study figs, you will end up studying wasps." -J.T. Wiebes, Curator of the Museum of Natural History and Chairman of the Department of Zoology, Leiden, Netherlands, 1954–1998

"If you study the wasps, you will end up studying their figs." -Finn Kjellberg, current Directeur de Recherche au Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier, France

"If you study figs, you will end up studying the animals that eat them" -Various

Figs (*Ficus* spp.) depend on wasps for transmission of their pollen and, therefore, viable seed production, whereas fig wasps depend on fig inflorescences for the completion of their life cycle. This relationship, fundamental to the reproduction of both parties, has extraordinary ecological consequences. From pea- to peach-sized or larger, the fruits of different fig species may ripen red, yellow, green, or purple, and may attract any of a wide range of frugivores, by either visual or chemical signaling (Berg & Wiebes 1992, Borges et al. 2008, Corner 1952, Harrison 2005, Kalko et al. 1996). Figs are truly keystone resources that provide the metabolic foundation for the pollinator and parasitic wasps, nematodes, mites, etc., that live within the microcosm of their fruit (Corner 1952, Compton et al. 1994). Figs also provide keystone resources at larger scales for communities of folivorous and frugivorous vertebrates and invertebrates, as well as the carnivores and insectivores that, respectively, eat them (Harrison 2005, Kalko et al. 1996, Korine et al. 2000, Shanahan et al. 2001). Figs exhibit a wide range of life forms (trees, shrubs, stranglers, vines), and occupy a diversity of habitats (rainforest understories and canopies, savannahs, riversides, xeric cliff faces) (Corner 1952, Harrison 2005, Janzen 1979). Reflecting this broad habitat range, figs show considerable variation in hydraulic properties and physiological adaptations (Patiño et al. 1994), including some of the highest photosynthetic rates recorded in nature (Zotz et al. 1995).

The sexual systems of figs are intriguing from several perspectives. Different species can be either monoecious or dioecious, with either active or passive pollination (Jousselin & Kjellberg 2001, Kjellberg et al. 2001, Machado et al. 2001, Weiblen 2004). The associated wasps show different types of sexual competition that range from females fighting to sex allocation shifts to lethal combat among sons (Hamilton 1997, Herre 1985, Moore et al. 2006, West et al. 2001). Genetically, figs generally exhibit extreme outbreeding and are highly heterozygous (Nason et al. 1998). Pollen dispersal (via their minute, short-lived wasps) can occur over extremely long distances, particularly in monoecious species, and their documented neighborhood sizes (hundreds of individuals) and effective gene flow (over hundreds of square kilometers) are among the highest known in plants (Harrison 2003, Harrison & Rasplus 2006, Nason et al. 1998, Zavodna et al. 2005; S.G. Compton, personal communication). Nonetheless, the population sizes of the wasps dwarf those of their hosts, and exhibit an alternation of variable, but generally extreme, inbreeding in the fruits, followed by extreme panmixis during dispersal (Herre 1985, Molbo et al. 2004, West et al. 2001). Figs are also prodigious colonizers that often initiate tropical forest succession with many well-documented cases of extensive seed dispersal (Thorton et al. 1996). All in all, figs and their wasps present a fascinating collection of attributes.

The fig-wasp interaction also presents numerous exciting experimental, observational, and comparative opportunities. For example, the basic currencies that constitute the costs and benefits for each partner can be measured. For the pollinator wasps, it is often possible to count the total number of sons and daughters of individual mothers (foundresses) that pollinate and lay eggs in a given fig inflorescence (Herre 1996; Molbo et al. 2003, 2004). This is not trivial if a researcher is interested in directly assessing the lifetime reproductive success (or sex allocation) of an individual.

For the fig, seeds and female pollinator wasps in ripe or nearly ripe fruits can be counted (Herre 1989). The former represents a major component of the fig's "female" reproductive success; the latter represents a major component of the fig's "male" reproductive success. Therefore, it is possible to estimate how each partner's success varies as a function of characters of the wasp (body size, foundress number, species identity, or even genetic makeup), of the fig (fruit or seed dry weight, number of flowers per inflorescence, resource availability, stage of receptivity, etc.), of both (foundress number, proportion of crop pollinated), or of neither the fig nor the wasp per se (levels of nematode, *Wolbachia*, or nonpollinator wasp infestation) (Bronstein 1988, 1991; Cook & Power 1996; Herre 1989, 1993, 1996; Kerdelhué & Rasplus 1996a, Pereira & Prado 2005, Shoemaker et al. 2002, West & Herre 1994). Measurements of the fitness consequences of these interactions demonstrate and often quantify the inherent tensions and trade-offs within the mutualism (Anstett et al. 1996, Harrison & Yamamura 2003, Herre 1989, Herre & West 1997, Patel & Hossaert-McKey 2000, Peng et al. 2005). With some intriguing exceptions, the interests of the fig generally appear to dominate the interaction (Harrison et al. 2008, Herre 1989, Jouselin et al. 2003a, Kerdelhué & Rasplus 1996b, Tarachai et al. 2008).

Here we discuss: 1) some essential natural history, 2) fig interactions with frugivores, 3) phylogenetic patterns of coevolution between figs and wasps, 4) effects of population structure, 5) maintenance of mutualism stability, 6) processes of coevolution between the figs and their pollinators, and 7) past and future research directions.

1. NATURAL HISTORY OF THE FIG AND POLLINATOR WASP (AND ASSOCIATES)

The fig inflorescence (syconium) defines the genus and presents a distinctive enclosed structure with scores to hundreds of uniovulate flowers oriented with their stigmatic surfaces pointed toward the interior. Approximately half of all fig species are functionally monoecious, with individual inflorescences performing both female (seed production and dispersal) and male (pollen production and dispersal) functions. In these systems, mated, pollen-bearing female fig wasps (foundresses) enter the syconia via a bract overlain pore called the ostiole, pollinate and/or oviposit in some number of the receptive flowers inside, and die, often without leaving. The relative style length varies, with the longer-styled flowers more likely to support the development of a seed, and the shorter ones more likely to support a wasp. In the process of oviposition, the foundress wasps apparently induce the formation of galls in the fig ovules (Jouselin et al. 2001a, Pereira et al. 2007, Verkerke 1989). Each pollinator wasp offspring then develops within a single, galled ovule that otherwise could potentially develop as a viable seed (Herre & West 1997). Just prior to final ripening of the fruit, the males emerge and mate with females still inside their galls. Male fig pollinating wasps are wingless and usually do not leave their natal fig (but see Greeff et al. 2003). The winged female offspring then obtain pollen from male flowers within the syconia, fly to a receptive fig tree, and thus begin the cycle anew (Corner 1952, Ramirez 1970).

In monoecious figs (which appears to be the basal condition for figs; Berg 1989, Machado et al. 2001), usually 40–50% of the flowers that develop produce viable seeds (Cook & Power 1996, Dunn et al. 2008, Herre 1989, Herre & West 1997, Kerdelhué & Rasplus 1996a). These seeds represent a large portion of the fig's investment in female function. Those flowers that support the development of the pollinator wasps (in particular the female wasps) represent a large portion of the fig's investment in male function (Herre 1989, 1996; Herre & West 1997). Individual female foundresses fertilize the flowers using the pollen from their natal syconium, thereby realizing male fitness for their own natal fig tree. Yet they then reproduce at the cost of some potential seeds (Herre 1989, 1999; Herre & West 1997). This inflicts a cost to the male success of their natal tree,

as well as inflicts a cost to the female success of the tree they pollinate (Herre 1999, Herre & West 1997). Nonetheless, where costs and benefits to each partner have been quantified, it appears that the fig's interests generally dominate (Herre 1989).

The remaining *Ficus* species are functionally dioecious. In these species some individuals produce only seed-bearing fruit, and are functionally female, whereas others produce only pollen and pollen-carrying wasp progeny, and are functionally male (Kjellberg et al. 1987, Patel & Hossaert-McKey 2000, Wiebes 1979). To complete the wasp life cycle, female wasps must enter a syconium on a male fig tree to produce offspring, whereas seed production requires that they enter and pollinate a female fig. For the wasp, entering a syconium on a female fig tree is a dead end, because that foundress cannot reproduce (Kerdelhué & Rasplus 1996b, Kjellberg et al. 1987, Patel 1996, Ramirez 1969, Wiebes 1979). Thus, the different breeding systems impose profoundly different reproductive consequences on both the host fig and the pollinator wasp (Grafen & Godfray 1991; Herre 1989, 1999; Kjellberg et al. 1987; Machado et al. 2001; Wiebes 1979). The fact that female figs continue to be pollinated is another, even clearer, example of the domination of fig interests.

The basis of host recognition in all fig pollinating wasps is due in large part to chemical attractants that the figs release when receptive (Borges et al. 2008, Grison-Pige et al. 2002a,b, van Noort et al. 1989, Ware et al. 1993). Different host species appear to produce different blends that the associated wasps recognize. Genetic work has shown that the pollen-bearing wasps routinely disperse many kilometers, with the result that the areas covered by effective breeding populations of figs are often on the order of a hundred or more square kilometers, an order of magnitude larger than that documented for any other plant species (Nason et al. 1998; also see Compton 1990, 1993; Harrison & Rasplus 2006; Ware & Compton 1992; Zavodna et al. 2005). Interestingly, different Asian wasp species preferentially show diurnal or nocturnal dispersal and typically fly at different heights in the canopy. Some dioecious species apparently exhibit relatively restricted pollen dispersal compared with sympatric monoecious fig species (Harrison 2003, Harrison & Rasplus 2006).

Across different species of figs and wasps, both active and passive pollination occurs. These different pollination syndromes are associated with distinctive morphological adaptations in both the wasp and the fig. Passively pollinated figs (apparently the basal condition) have relatively high ratios of anthers to female flowers and produce much more pollen per syconium than do actively pollinated figs, and their mature anthers tend to dehisce naturally, facilitating the passive collection of pollen by their pollinators (pollen adheres to various parts of the body surface) (Jousselin et al. 2003a, Kjellberg et al. 2001). The wasps that passively pollinate their hosts show no active pollination behavior (Kjellberg et al. 2001, Ramirez 1969). In contrast, the male flowers in actively pollinated figs are relatively small and less numerous (Kjellberg et al. 2001), and the wasps possess specialized structures to carry pollen in the external part of the thorax and the front legs (Galil & Eisikowitch 1969, Ramirez 1969) and show distinctive behaviors for collecting and depositing pollen (Frank 1984, Galil & Eisikowitch 1969). Thus, passive pollination appears to be relatively costly for the fig (in pollen) and relatively advantageous for the wasp (no specialized pollen structures or active behaviors) (Kjellberg et al. 2001, Machado et al. 2001).

Although authors previously tended to emphasize pollinator-host fig specificity, there are many reports of what are thought to be single fig species pollinated by two or more species of wasps (based on wasp morphology) (Berg & Wiebes 1992, Michaloud et al. 1996, Rasplus 1996). Further, recent genetic work based on extensive sampling of wasps associated with several Neotropical host fig taxa has revealed the presence of previously undetected cryptic pollinator species (Molbo et al. 2003). In stark contrast to the prevailing perception, in cases where groups of host figs have been studied in detail, most species (~50%) are routinely pollinated by more than one wasp species (Haine et al. 2006; Lopez-Vaamonde et al. 2001, 2002; Machado et al. 2005; Molbo et al. 2003;

Su et al. 2008; G. Weiblen, personal communication). In some cases, the more common wasp species associated with a particular fig host may routinely comprise 80% to 90% of the foundresses. In other cases, there is no “more common wasp species,” and the different wasp species alternate as the most common pollinator of a given crop. Further, in some cases, what appear to be genetically indistinguishable wasps pollinate different host fig species (Machado et al. 2005). Finally, in some cases, different individuals of what appear to be the same host fig species are routinely pollinated by different wasp species, suggesting the existence of “cryptic” fig species (Molbo et al. 2003, 2004; D. Molbo & E.A. Herre, unpublished data). These findings undermine the long-held one to one fig-pollinator interaction and add previously unsuspected levels of complexity to the mutualism (Jackson et al. 2008, Joussein et al. 2003b, Kerdelhué et al. 1999, Machado et al. 2005, Molbo et al. 2003, Peng et al. 2008, Su et al. 2008).

Figs also support a diverse community of nonpollinating wasps that are generally parasitic on some of the products of the fig-pollinator mutualism. A great deal of research effort has been devoted to three aspects of the nonpollinators: phylogeny; ecology; and the extreme polymorphisms observed between the sexes and among males, and their penchant for lethal combat (Boucek 1988; Bronstein 1991; Compton & Hawkins 1992; Compton & van Noort 1992; Compton et al. 1994; Cook & Bean 2006; Cook & Power 1996; Hamilton 1997; Joussein et al. 2006; Kerdelhué & Rasplus 1996a; Kerdelhué et al. 2000; van Noort & Compton 1996; West & Herre 1994; West et al. 1996, 2001).

Recent molecular studies have shown that the Agaonidae, defined by Boucek (1988) as the family that contains all pollinating and most nonpollinating fig wasps, is paraphyletic (Machado 1998, Rasplus et al. 1998). Three of the constituent subfamilies of nonpollinating fig wasps (Sycocinae, Otitesellinae, and Sycoryctinae) were reassigned to the family Pteromalidae, and the pollinating fig wasps were left in their own family, Agaonidae (Campbell et al. 2000, Rasplus et al. 1998). The taxonomic affinities of subfamilies Sycophaginae and Epichrysomalinae are currently unclear, but they clearly do not belong in the Agaonidae (J.Y. Rasplus, S. van Noort, personal communication). Data collected in Asia (Weiblen & Bush 2002) and in Panama (Marussich & Machado 2007) suggest that nonpollinators are generally less specific to the host fig than pollinators. Interestingly, molecular data from some African figs suggest otherwise (Joussein et al. 2006, 2008).

In the New World, all known nonpollinating wasp species oviposit from the surface of the syconium. These externally ovipositing wasps seem to comprise three very ecologically distinct groups that, in several cases, have ecological counterparts in Old World fig systems (Compton & van Noort 1992, Compton et al. 1994, Harrison et al. 2008, Kerdelhué & Rasplus 1996a, Kerdelhué et al. 2000, Marussich & Machado 2007, West et al. 1996). The first group is similar in body size to the pollinators and appears to primarily compete with them for the individual flowers that provide larval resources, usually reducing the production of pollinator offspring (e.g., *Critogaster* and some groups of *Idarnes*; West & Herre 1994, West et al. 1996). These wasps have little effect on seed production (but see Pereira et al. 2007). Further, some evidence suggests that these nonpollinators affect pollinator sex ratios by differentially reducing pollinator female production (Pereira & Prado 2005). The second group of relatively larger wasps lays their eggs in the flowers or fruit walls, inducing the formation of large galls in which the larvae develop, and seem to prevent unpollinated fruit from being aborted [e.g., *Aepocerus* and *Idarnes* (incerta)]. These wasps drain resources from the fig, and thereby reduce both pollinator and seed output (West et al. 1996). The third is a group of true parasitoids of the larger gall-formers (e.g., *Physothorax*) (West & Herre 1994, West et al. 1996). Finally, in addition to wasps of these ecological types, some Old World nonpollinators enter the syconia to oviposit (internal ovipositors). These wasps include all members of the subfamily Sycocinae, three genera from the subfamily Otitesellinae (*Eujacobsonia*, *Lipothymus*, *Grasseiana*), one undescribed member of the subfamily Epichrysomalinae, and the genus *Sycophaga* from the

subfamily Sycophaginae (Boucek 1988, van Noort & Compton 1996). Studies of nonpollinators that enter the syconium to oviposit, pollinators, and their host figs suggest either tight cospeciation or else provide an exceptional case of convergent evolution (van Noort & Compton 1996).

Interestingly, in the vast majority of cases, externally ovipositing nonpollinators that are associated with dioecious species exploit the syconia of only the male trees, thereby usually reducing the production of pollinator offspring (Harrison & Yamamura 2003, Kerdelhué & Rasplus 1996b, Yu et al. 2008). This is directly analogous to results in monoecious figs that show nonpollinators largely reducing male success via reduced pollinator production (West & Herre 1994, West et al. 1996). However, a few cases are known in which nonpollinators exploit flowers that normally produce seeds in the female fruit (Y.-Q. Peng & J.-Y. Rasplus, personal communication). Further, within recognized genera there are shifts in ecology and larval diets of the nonpollinating wasp taxa (Cook & Power 1996, Harrison et al. 2008, Machado 1998, Peng et al. 2005, Pereira et al. 2007, West et al. 1996). Moreover, evidence shows that some nonpollinating wasps that enter the syconium (internal ovipositors) in passively pollinated figs can provide pollination services, and have effectively made a transition from parasite to mutualist (Jousselin et al. 2001b). Ultimately, the ecological effects, community assembly, and evolutionary relationships of nonpollinators (gall formers, inquilines, parasitoids, hyperparasitoids) are still only imperfectly understood and a great deal more work is needed (Compton et al. 1994, Harrison et al. 2008, Jousselin et al. 2008, Machado 1998, Peng et al. 2005, Pereira et al. 2007, West et al. 1996).

One fascinating attribute of nonpollinating fig wasps is male polymorphism. In some species, males can be either wingless and mate exclusively in or near the natal fig, or winged and capable of flight. Further, in many of the cases in which the males are wingless, males form a continuum with large fighting morphs at one extreme and small “sneaker” morphs at the other (Cook & Bean 2006, Hamilton 1997, Murray 1990). Recent work shows that in at least one case the mother apparently determines the different male morphologies (Pienaar & Greeff 2003). The fact that these morphs tend to evolve independently and change frequently even among closely related species (Jousselin et al. 2004b) suggests relatively rapid responses to selection on male morphs and behavior in these systems. Hamilton (1997) proposed that selection for the male polymorphism was likely due to different potentials for brothers to directly compete with each other for mates, and that the lower the relatedness among con-specific males, the more likely they would exhibit morphological and behavioral adaptation for lethal combat. West et al. (2001) argued that expected opportunities for mates for males in a given species (absolute number of females in a given syconium) was more important than relatedness in predicting the presence and intensity of lethal combat and presented a phylogenetic analysis consistent with that interpretation. However, the presence of cryptic pollinator and nonpollinator species, as well as the discovery of male dispersal and fighting in pollinators, suggests that this issue should be revisited (Greeff et al. 2003, Jousselin et al. 2006; F. Kjellberg and J.-Y. Rasplus, personal communication).

2. COMMUNITY PATTERNS OF FRUGIVORY

Shanahan, Harrison and colleagues (2001) supported previous claims that *Ficus* is probably the most important plant genus for tropical frugivores. Further, Kissling and collaborators (2007) found that the species richness of *Ficus* had the strongest direct effect on species richness patterns of avian frugivores across sub-Saharan Africa. These and other studies support the claim that, even at continental scales, figs are keystone resources for animal consumers. Consistent conclusions have been reached in studies conducted at much smaller spatial scales (Adler 2000). Contrary to some previous perceptions, nutrient analyses show that figs often provide high-value fruit (e.g., high calcium) (O'Brien et al. 1998, Wendeln et al. 2000; also see Harrison 2005, Shanahan et al.

2001). Asynchronous fruiting among individuals of many fig species means that fig fruits will be available during most times of the year and are thus usually a dependable resource (Shanahan et al. 2001). Studies in both the Old and New World tropics now indicate that the relationships between particular figs and their suite of frugivores are much more specific than previously appreciated (Kalko et al. 1996, Korine et al. 2000, Shanahan et al. 2001). Historical records and ongoing studies show that figs have played a central role in enhancing forest recolonization on the Krakatau islands after the 1883 volcanic eruption that extirpated life there (Thorton et al. 1996).

Finally, the frugivores exert considerable selection on figs, to the point of negatively affecting characters involved with pollination. Specifically, in a study conducted in Central Panama, larger-fruited figs are preferred by larger bat species (Kalko et al. 1996). However, larger fruit size in monoecious species is associated with numerous inefficiencies and costs. Specifically, larger-fruited fig species are generally characterized by higher average numbers of foundresses. Higher foundress numbers, in turn, correlate strongly with less female-biased sex ratios in the pollinators, which results in less efficient production of the winged pollinator females that disperse fig pollen (Herre 1985, 1989, 1996). Further, the nematodes associated with figs that produce higher foundress numbers exhibit higher levels of virulence, further reducing the efficiency of pollen dispersal (Herre 1993, 1996). Finally, the need to keep fig fruits cool enough to prevent the overheating of developing wasps combines with the physical constraints of higher surface to volume ratios to impose a higher hydraulic cost in larger-fruited figs (Herre 1996, Patiño et al. 1994). The multiple inefficiencies associated with these larger-fruited fig species can potentially be balanced by advantages to seed dispersal through larger travel distances by the larger-bodied frugivores that typically prefer to consume larger fruit (Herre 1996, Kalko et al. 1996; E. Kalko, unpublished data).

3. PATTERNS OF FIG AND WASP PHYLOGENETIC COEVOLUTION

The fig-wasp mutualism is both ancient and diverse, originating roughly 70–90 mya, before the breakup of Gondwana (Corner 1952; Machado et al. 2001; Rønsted et al. 2005, 2008), with more than 750 extant species of figs currently recognized (Berg 1989, Wiebes 1979). Both morphological and recent molecular studies broadly support the proposition of cocladogenesis and coadaptation at a coarse systematic scale (i.e., between recognized genera of pollinating wasps and their respective sections of figs) (Berg 1989; Berg & Wiebes 1992; Corner 1985; Joussetin et al. 2003b; Machado et al. 2001; Ramirez 1970, 1974; Rønsted et al. 2005, 2008; Weiblen 1999, 2000, 2001, 2004; Wiebes 1979) (**Figure 1**). However, at a finer scale, there is little evidence from appropriately detailed studies to support strict cospeciation (Jackson et al. 2008, Joussetin et al. 2008, Machado et al. 2005; but see Weiblen & Bush 2002), and even the paradigm of a predominance of one species of pollinator wasp to one fig species is doubtful (Haine et al. 2006, Lopez-Vaamonde et al. 2002, Machado et al. 2005, Marussich & Machado 2007, Molbo et al. 2003, Su et al. 2008).

Although the relationships among some taxonomic sections of *Ficus* are not well resolved (Joussetin et al. 2003b; Rønsted et al. 2005, 2008), monoecy was clearly the ancestral breeding system and the ancestral pollination mode was passive (**Figure 1**). Furthermore, both breeding system and pollination mode have shown shifts and even reversals throughout the history of the fig-wasp mutualism (**Figure 1**). At least two independent transitions to dioecy occurred, with possible reversals to functional monoecy (Berg 1989, Joussetin et al. 2003b, Rønsted et al. 2008). The specialization in sexual function that is characteristic of dioecy may be favored by inherent inefficiencies of a single fig fruit to engage in both male and female sexual functions simultaneously (Herre 1989, 1996). Some ecological circumstances have been suggested to favor different aspects of these tradeoffs, and thereby favor either monoecy or dioecy (Borges et al. 2008; Harrison &

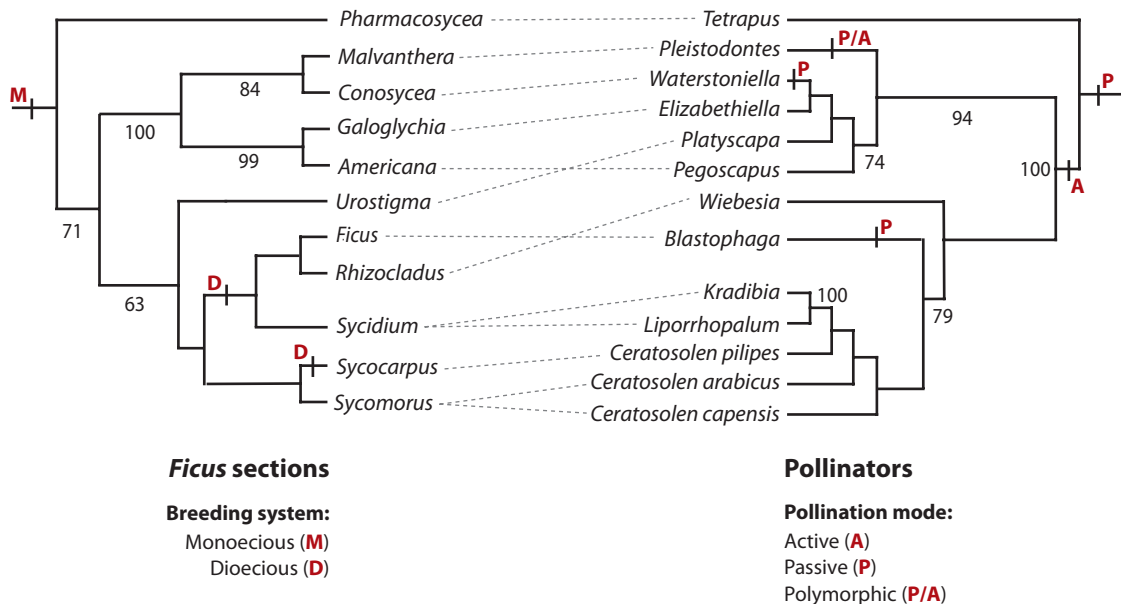


Figure 1

Cophylogenetic history of the main sections of *Ficus* and their associated genera of pollinating wasps. Breeding system and pollination mode are mapped on the trees. Transitions from monoecy (M) to dioecy (D) and from passive (P) to active (A) pollination are shown. Phylogenies represent pruned trees from larger phylogenetic studies (Machado et al. 2001, Rønsted et al. 2005, Weiblen 2000). (C has been spelled out in the figure.) Monoecy and passive pollination are ancestral in figs and pollinators, respectively. Numbers associated with branches are bootstrap values >40% that were taken directly from the studies in which the complete phylogenies were originally presented (Machado et al. 2001, Rønsted et al. 2005, Weiblen 2000).

Yamamura 2003; Herre 1989, 1996; Kalko et al. 1996, Patel & Hossaert-McKey 2000, Patiño et al. 1994, Yu et al. 2008). Further, passive pollination is the ancestral behavior and a single inferred change from passive to active pollination occurred among sections of figs and their associated wasps, with several independent reversals to passive pollination (Jousselin et al. 2003a,b, Machado et al. 2001) (**Figure 1**). Interestingly, within the predominantly Australian section *Malvanthera*, Cook et al. (2004) have described the fascinating case of the complex suite of characters of both partners apparently switching back and forth between active and passive pollination.

4. POPULATION STRUCTURE AND ITS EFFECTS

William Hamilton (1997) wrote that sex allocation in general, and local mate competition in particular, is “the section of evolutionary theory that best proves the power and accuracy of the Neodarwinian paradigm as a whole.” Perhaps no group of organisms has contributed as much in terms of the development of the initial theory, or the subsequent testing of it, than the different groups of wasps that are associated with figs. Fig wasps vary considerably in the number of foundresses that oviposit within a single fruit, the degree to which males are confined to mating within the fruit within which they are born, and therefore, the degree to which local mating and sexual competition takes place between related individuals (i.e., population structure). As theory predicts, fig-pollinating wasps usually show a female-biased sex ratio, the capacity to adaptively shift sex ratios (in response to different numbers of foundresses), and remarkable precision of their sex ratio responses (Frank 1985; Hamilton 1997; Herre 1985; Molbo et al. 2003, 2004;

Pereira & Prado 2005; Pienaar & Greeff 2003; West & Herre 1998; West et al. 2001; Yu et al. 2008). More broadly, we note that by resolving cryptic wasp species, interpretations of sex ratio adaptations (population mean sex ratios and adaptive sex ratio shifts) are still well supported, and the fit between observed and predicted brood sex ratios appears to be even more precise than previously recognized (Molbo et al. 2003, 2004). Nonetheless, further advances in studies of sex ratio adaptations and other forms of sexual competition will depend on correctly identifying cryptic wasp species, and correctly assigning offspring to their respective mothers.

Finally, the natural histories of fig-pollinating wasps and the nematodes that parasitize them permit the direct measurement of several parameters that theory identifies as important to the evolution of virulence (Herre 1993). Those species with a high number of foundresses consistently present their parasitic nematode populations with relatively greater opportunities for horizontal transmission, and these situations correspond to the greatest estimated levels of virulence (Herre 1993). Interestingly, both of these effects of increased foundress number (less female-biased sex ratios and increased nematode virulence) are detrimental to the male component of the fig's reproductive success (Herre 1985, 1989, 1993, 1996). Moreover, given the different population sizes and structures that characterize the figs, the different wasps and nematodes provide remarkable opportunities to study the factors that shape fundamental processes in molecular evolution, such as levels of genetic diversity and heterozygosity as well as rates of silent and expressed mutations (Jackson et al. 2008; Machado 1998; Machado et al. 2005; Molbo et al. 2003, 2004).

5. MECHANISMS UNDERLYING STABILITY IN THE FIG-WASP MUTUALISM

The complex interdependencies and conflicts of interest between species in the fig microcosm pose several questions concerning what factors promote and maintain stability in the mutualism (Bronstein 1988; Cook et al. 2004; Herre 1989, 1996, 1999; Jousset et al. 2003a; Kjellberg et al. 2001; Weiblen 2004). Perhaps the most obvious question is how do figs receive a dependable supply of pollinator wasps, given that wasps live for only a day or two after emergence? Individual fig species often grow at very low densities, and they usually exhibit phenological patterns in which individual trees flower (produce receptive syconia) roughly synchronously within its crown, but different individual trees flower asynchronously (Janzen 1979, Nason et al. 1998). However, there are cases in which individual trees produce crops asynchronously such that wasps leaving one fruit could enter and pollinate another syconium on the same tree (Cook & Power 1996, Hossaert-McKey & Bronstein 2001). Nonetheless, the extraordinarily high heterozygosities usually found in adults indicate a routine advantage to outcrossed fig offspring (Nason et al. 1998; J. Nason, personal communication). These observations suggest that huge population sizes of figs are required to avoid a chronic shortage of pollinators (Hossaert-McKey & Bronstein 2001, Janzen 1979). Genetic studies have confirmed this inference, showing that dispersal distances for fig wasps are perhaps the largest known in plants (Nason et al. 1998; also see Compton 1990, 1993; Ware & Compton 1992; Zavodna et al. 2005). Moreover, by signaling their pollinators via volatile chemicals, figs add a considerable degree of specificity to their already extraordinary dispersal. Indeed, across fig species studied in central Panama, roughly 1 in 100 emerging female wasps encounters a receptive fig (Herre 1989). At larger scales, studies documenting the local extirpation of wasp populations after hurricanes in Florida (Bronstein & Hossaert-McKey 1995) and droughts in Southeast Asia (Harrison 2003, 2005) show that these populations have a remarkable capacity to rebound, presumably via long distance colonization.

A second question that has attracted a great deal of interest has been how wasps are prevented from exploiting all flowers in monoecious figs. Contrary to the situation in the mutualism

between yuccas and their moths (Pellmyr & Huth 1994), there is little evidence that figs routinely abort overexploited fruit (Galil & Eisikowitch 1971, Joussetin & Kjellberg 2001, Joussetin et al. 2003a, Nefdt 1989, Tarachai et al. 2008; R. Harrison, personal communication). Instead, it appears that figs possess mechanisms that prevent overexploitation during oviposition. Pollinator wasps oviposit through the style into the ovule (Galil & Eisikowitch 1969, Verkerke 1989), and their offspring preferentially develop in shorter-styled flowers, closer to the fig lumen, whereas seeds preferentially develop in longer-styled flowers with ovules closer to the syconium's outer wall (Anstett 2001, Dunn et al. 2008, Galil & Eisikowitch 1969, Herre 1989, Joussetin et al. 2001a, Nefdt & Compton 1996, Verkerke 1989, West & Herre 1994). However, hypotheses suggesting that the relative lengths of pollinator ovipositors and fig styles are the main factors that prevent overexploitation of flowers by the wasps cannot be generalized across monoecious species. Measurements of styles and pollinator ovipositors show that most ovules in most monoecious species are within the wasps' reach (Bronstein 1988, Kathuria et al. 1995, Nefdt & Compton 1996, Otero & Ackerman 2002). Possibly there are chemical or physical differences among flowers that often correlate with style length, and these differences tend to prevent a portion of them from receiving eggs or make them less conducive to supporting wasp development (Herre & West 1997, Verkerke 1989, West & Herre 1994, West et al. 1996; S.G. Compton, personal communication). For example, stigma morphology that correlates with style length seems to explain preferential oviposition in short-styled flowers in the passively pollinated *Pharmacosycea* figs. In *Ficus maxima* (as with other *Pharmacosycea*) long-styled flowers have slender stigmas that protrude into the fig cavity, facilitating pollen deposition while making oviposition less likely (Joussetin et al. 2004a, E.A. Herre & K.C. Jandér, personal observations).

Further, as with the pollinators, many externally ovipositing nonpollinators in the New World figs also tend to develop in shorter-styled flowers closer to the interior of the fruit (Compton et al. 1994, Herre 1989, West & Herre 1994). This phenomenon suggests that the longer-styled flowers are not (or less) available for either pollinator or nonpollinator wasps to exploit (Anstett 2001, Dunn et al. 2008, Herre & West 1997, Pereira et al. 2007, West & Herre 1994). However, examples exist of parasitic wasps that develop in long-styled flowers (Cook & Power 1996, Dunn et al. 2008, Galil & Eisikowitch 1969, Kerdelhué et al. 2000, Pereira et al. 2007, West et al. 1996), implying that this hypothesis is not general to all fig species, or that some parasitic wasps have circumvented the fig's defense.

Other hypotheses suggest constraints on egg number, ovipositor length, spacing of galls, or time for oviposition in the fig (Anstett 2001, Compton 1993, Ganeshaiyah et al. 1995, Kathuria et al. 1995, Yu et al. 2004). For example, in a study of several African figs, foundresses on average did not carry enough eggs to use all accessible ovules (Nefdt & Compton 1996). Although true for some African species, this insufficient-egg-supply hypothesis cannot be a general explanation because there are numerous fig species where the total number of eggs in foundresses often greatly exceeds flower number (Anstett et al. 1996, Herre 1989). A short wasp life span may also limit oviposition opportunities, selecting for preferential oviposition in shorter-styled flowers that possibly require less processing time per egg laid (Yu et al. 2004). Although this theoretical model can be parameterized to fit some cases, it does not offer a general explanation of why not all ovules are used when many foundresses are present. It is also puzzling why pollinator wasps would not evolve a longer life span.

Finally, it was recently suggested that the direct threat of parasitism from nonpollinators to developing pollinators increases with style length, and that this effect selects against the pollinators ovipositing in longer-styled flowers (Dunn et al. 2008; also see Cook & Power 1996, Yu et al. 2004). However, this hypothesis should be viewed with caution, because this study lumped together different genera of nonpollinators that other studies have shown not to directly parasitize

pollinators, and the proportion of flowers that developed was remarkably low compared with the number of eggs that the pollinators typically carry (Cook & Power 1996, Herre 1989, Kerdelhué & Rasplus 1996a, Peng et al. 2005; also see Pereira et al. 2007). To adequately test this idea, studies that (a) directly address larval diets of the different nonpollinator species (e.g., Pereira et al. 2007, West et al. 1996), and (b) document the actual distribution of pollinator and nonpollinator oviposition sites across flowers with different style lengths (e.g., Jusselin et al. 2001a) are needed. Nonetheless, in monoecious fig species, with few exceptions shorter-styled flowers preferentially support the development of wasps of many different kinds and longer-styled flowers preferentially support the development of seeds. In any event, one very intriguing possibility is that different fig-wasp systems have achieved stability through different mechanisms.

A third question is why wasps in actively pollinated systems actually pollinate at all. Pollination is the central service that the wasp provides to the fig, and the stability of the mutualism depends in part on this service (Jusselin & Kjellberg 2001, Jusselin et al. 2003a, Kjellberg et al. 2001). Yet, active pollination requires time and energy on the part of the wasps. Do wasps benefit from pollinating the figs? Unpollinated figs have been suggested to be selectively aborted by the tree, thus killing the wasp larvae inside. Although selective abortion of nonpollinated fruits is well documented in yuccas (Pellmyr & Huth 1994), this mechanism was not shown in any fig species until recently (see **Table 1**, Tarachai et al. 2008).

In several fig species, both correlational and experimental studies have suggested that wasps that pollinate have more offspring. Herre & West (1997) showed that pollinators generally have the highest reproductive success in the fruits that also show the highest seed production. Where these increases in seed production are linked to increased pollination (both wasp and seed production are correlated with increased proportion and number of flowers that developed), the wasp's reproductive success is tied to its capacity to pollinate (Herre 1989, 1999; Herre &

Table 1 Results from experiments with pollen-carrying or pollen-free wasps in *Ficus*^a

Species ^b	Number of trees tested	No-pollen treatment		Pollen treatment		p-value	Reference
		Mean wasp offspring per fig (SD)	Number of fig fruits	Mean wasp offspring per fig (SD)	Number of fig fruits		
Monoecious							
<i>Ficus religiosa</i>	3	no data presented	“large”	no data presented	no data presented	no test presented	Galil & Eisikowitch 1971
<i>F. sur</i>	1	102	3	193	4	0.04	Nefdt 1989
<i>F. burtt-davyii</i>	1	43 (17)	12	66 (16)	6	0.015	Nefdt 1989
<i>F. microcarpa</i>	1	32 (27)	7 (+4 aborted)	63 (36)	8 (+4 aborted)	0.066	Jusselin et al. 2003a
Dioecious							
<i>F. condensa</i>	1	67 (57)	13 (+3 aborted)	110 (55)	13 (+3 aborted)	0.03	Jusselin & Kjellberg 2001
<i>F. montana</i>	1	28 (16)	12 (+48 aborted)	57 (15)	30 (+30 aborted)	<0.001	Tarachai et al. 2008

^aMeans and standard deviations are rounded to integers.

^bData presented for *F. sur* are based on fig fruits with two foundresses because sample sizes for figs with single foundresses were too small to perform any statistical tests (Nefdt 1989); all other studies used single foundresses. SD, standard deviation.

West 1997). Several experimental studies have introduced pollen-free (P−) wasps into receptive fig fruits, and compared their reproductive success with pollen-carrying (P+) wasps (Galil & Eisikowitch 1971, Jousselin & Kjellberg 2001, Jousselin et al. 2003a, Nefdt 1989, Tarachai et al. 2008). Although the sample sizes are generally not large, published studies all suggest that wasps that do not pollinate pay a fitness cost in active pollination systems (**Table 1**).

Until very recently, only one case of a pollinating wasp species evolving into a nonpollinating parasite was known. *Ceratosolen galili* is associated with *Ficus sycomorus*, an African fig that is normally pollinated by *C. arabicus*, an active pollinator. Although *C. galili* has pollen pockets, suggesting an origin as an active pollinator, it has lost the behavior associated with active pollination (Compton et al. 1991, Galil & Eisikowitch 1969). Further, phylogenetic analyses suggest that *C. galili* (or its ancestor) successfully colonized *F. sycomorus*, and then became a parasitic “cuckoo” (Kerdelhué et al. 1999). This “colonization by a nonsister taxa” scenario mirrors patterns observed among mutualistic and parasitic lineages of yucca moths (Pellmyr et al. 1996). However, recent work in China has uncovered another similar case (Peng et al. 2008). In the host species *Ficus altissima*, there is a pollinator wasp *Eupristina altissima*, and an as yet undescribed, “cheater” (= “cuckoo”) *Eupristina* sp. Analogous to the *F. sycomorus* case, the good (= “cooperative”) pollinator is an active pollinator and the cheater appears to have once been an active pollinator. In neither case does the development of cheater offspring depend on the good pollinator to pollinate the fig. However, in the Chinese case the congeneric cheater appears to be the sister species of the pollinating species (Peng et al. 2008; Y.-Q. Peng & J.-Y. Rasplus, personal communication).

The studies showing that P− wasps suffer reduced fitness (**Table 1**) and these two cases of cheating pollinators raise several questions. In both cases, the cheater does not depend on the presence of the good pollinator to exploit the flowers in a given syconium for the development of its offspring. That is, there is no direct hitchhiking on the pollination of the mutualist species. Have these two cheater wasps discovered some strategy for circumventing mechanisms that still provide effective sanctions that keep the good pollinator species pollinating? Or do these two host species that harbor cheaters exhibit no (or exceptionally weak) sanctions? These questions can be addressed by performing P+ and P− studies on the pollinators. If P− pollinator wasps show lower reproductive success compared with P+, then the fig tree has effective sanction mechanisms for the pollinator. In this case, the question becomes: why does the host’s sanction mechanism that works for the pollinator not work for its congeneric cheater? That is, what is the cheater’s trick? And why don’t other species, including the proper pollinator, learn this trick and circumvent the host’s interests? Conversely, if P− pollinator wasps show equal (or greater) reproductive success, this result suggests that these host trees do not have sanctioning mechanisms in place. In this latter case, the question becomes: why do these two host species lack sanction mechanisms? More broadly, such studies should be conducted on fig species that host internal nonpollinator wasps such as *Sycophaga*, in which the nonpollinators’ successful development apparently does not require the fig to be pollinated (van Noort & Compton 1996; S.G. Compton, personal communication). Ultimately, more detailed studies across both active and passive systems are needed to more clearly characterize evolution of the sanctioning mechanisms that seem to promote pollination.

6. PROCESSES OF COEVOLUTION AND COADAPTATION

Although groups of figs appear to usually coradiate with groups of wasps, these patterns at the section (figs) and genus (wasps) level do not necessarily tell us about the actual process of ongoing speciation and adaptation within figs and their related wasps. Several fine-scale studies from figs and wasps in many parts of the world cast considerable doubt on the generality of strict host specificity and strict cospeciation. Specifically, the inflorescences of single host fig individuals

are often pollinated by more than one wasp species, and different fig species sometimes share pollinator species (Haine et al. 2006, Machado et al. 2005, Molbo et al. 2003, Su et al. 2008; F. Kjellberg & G. Weiblen, personal communication). In some cases, these previously unrecognized (cryptic) wasp species that are associated with the same host are closest relatives. In other cases, the cryptic species pairs associated with the same host are not sibling species, which indicates a host switch. Further, in some cases, wasps that are genetically indistinguishable regularly pollinate what appear to be different host fig species. These findings from many parts of the world help make sense of other studies that suggest hybridization and genetic introgression among what appear to be different host fig species (Berg 1989, Machado et al. 2005, Parrish et al. 2003, Ramirez 1994; E.A. Herre & K.C. Jandér, personal observations).

A recent study critically tested the hypothesis of strict cospeciation (Jackson et al. 2008) using two nuclear loci from multiple individuals per species to evaluate the distribution of alleles within and among Panamanian fig populations, and found three main results. First, the two nuclear genes analyzed in detail agreed with other studies in finding deep genetic divergence between the *Pharmacosyceae* and *Americana* sections (Jackson et al. 2008; Jousselin et al. 2003b; Machado et al. 2005; Rønsted et al. 2005, 2008). However, very little genetic divergence was found among fig species within either section despite clear evidence that both sections are very old (Machado et al. 2001, 2005). Second, the two loci have clearly distinct evolutionary histories, and both genes possess multiple haplotypes that are not monophyletic by fig species. The latter result cannot be explained by paralogy because remarkable levels of gene duplication would be required to explain the observed patterns (Jackson et al. 2008). Third, despite clear, consistent phylogenetic resolution of the associated pollinator wasp species based on multiple genes sampled in multiple individual wasps, neither individual nor combined data sets in the figs support codivergence between the fig hosts and their associated wasp pollinators. None of these results is easily reconciled with the proposition of species specificity and strict cospeciation in the fig-wasp mutualism at this fine scale of sympatric species within a section. Finally, through ranges of sympatry, apparently fertile hybrids exist (Jackson et al. 2008, Machado et al. 2005; E.A. Herre, personal observations). Combined, these results indicate that there is the opportunity for gene flow among species. Indeed, conservative analyses suggest that hybridization and gene introgression have occurred among what we currently recognize as different fig species (Machado et al. 2005).

One interpretation of the very clear genetic and morphological divergence among the closely related pollinator wasps (with several congeneric species separated by more than five million years) coupled with the strikingly little genetic divergence among their associated fig species within sections is that wasp speciation often precedes fig speciation (Jackson et al. 2008, Machado et al. 2005, Rønsted et al. 2005). Indeed, results from two independent studies corroborate this interpretation. Each study found a strong positive correlation between the estimated speciation/divergence dates of groups of fig-pollinating wasps and those of their associated host figs. However, in both cases there are nonzero intercepts on the axis of the wasps, consistent with the interpretation that wasp speciation generally precedes the genetic differentiation and speciation events in the associated figs (Rønsted et al. 2005, Weiblen 1999; but see Silvieus et al. 2007). It would also appear that even after "speciation," there is a considerable lag in the fig genes sorting out by species. So, given what we know, what are some likely scenarios for fine-scale coevolution and coadaptation?

With respect to coevolution, pollinator choice of hosts (coupled with pollination success) determines patterns of host gene flow. This choice also determines what wasp individuals might be available as mates. Host choice appears to be largely based on the blends of volatile chemicals that the host fig species produces (Borges et al. 2008; Grison-Pige et al. 2002a,b; van Noort et al. 1989; Ware et al. 1993). We can expect an evolutionary positive feedback involving wasp choice and the chemistry of the attractant volatiles produced by the host (Kiestler et al. 1984, Machado

et al. 2005). Such positive feedback systems are analogous to processes of sexual selection, are thus conducive to speciation, and are therefore likely to promote the generation of taxonomic diversity such as is observed in figs and their wasps (Herre 1996, 1999; Kiester et al. 1984; Machado et al. 2005).

With respect to coadaptation, measurements of the reproductive benefits that each of the partners derives from their mutualistic interactions suggest that, with some intriguing exceptions that we have outlined (two cases of cheaters and several cases of internally ovipositing nonpollinators), fig interests generally dominate the interaction. In particular, we see that in most cases the pollinators that do not pollinate are punished (sometimes severely) and that, although there is an underlying negative correlation between seed and wasp production, the pollinators that pollinate best also produce more offspring (Herre 1989, Herre & West 1997) (**Table 1**). It follows that within a host fig species the pollinators that produce the most offspring will also transmit the most pollen and ultimately be most effective at transmitting the host genes that underlie the mechanisms that sanction cheaters and reward the best pollinators. We therefore have the makings of a second positive feedback involving stability mechanisms. As is the case with the volatiles, we expect that hybridization events can either disrupt effective sanction mechanisms or possibly produce new combinations. In both cases, we expect that selection on resulting hybrids will strongly influence patterns of genetic introgression (Machado et al. 2005).

The issues, then, are to determine the mechanisms of host control (which appear to be different in different systems; **Table 1**), and to understand whether breakdown is more likely due to innovations on the part of the cheating wasp (for example, if the P– pollinator wasps in *F. sycomorus* and *F. altissima* have lower fitness than the P+ pollinator wasps), or breakdowns on the part of the fig. (e.g., no evidence for any sanctions against P– wasps). The former might appear more likely in the case of *F. altissima* because the pollinator's apparent sister species is the cheater. The latter could result in the case of hybridization between two fig species with different sanction mechanisms, and would appear more likely in the case of *F. sycomorus*. Ultimately, it is desirable to more clearly establish the links among wasp choice in hosts, the chemistry of host volatile attractants, sanction mechanisms, selection on syconium properties that may be driven by frugivory and/or physiological constraints (fruit size, flower number, etc.), and host population genetics.

7. FINAL THOUGHTS

Thirty years ago Janzen reviewed and synthesized the existing studies of the ecology and evolution of figs and their associates (Janzen 1979). In particular, pioneering studies of: (a) phylogenetic relationships (Berg 1989, Berg & Wiebes 1992, Corner 1985, Ramirez 1974, Wiebes 1979), (b) pollination biology (Galil & Eisikowitch 1969, 1971; Ramirez 1969, 1970), (c) frugivory (Corner 1952, Janzen 1979), and (d) population structure, sex allocation, and sexual competition (reviewed in Hamilton 1997) set the stage for much of what has followed. This review shows that more recent work has greatly enriched those themes. However, much more has been accomplished than simply elaborating on preexisting research traditions. Basic changes in perceptions of natural history include the following: the recognition of cryptic species of pollinators, the improved resolution of the ecology and mating systems of other fig-associated wasps, the increasing appreciation of the role of volatile chemicals in pollinator and frugivore attraction, and the demonstration of the vast scales over which pollen and seed dispersal takes place. Importantly, these insights combined with the increasing influx of molecular information collected from all the associated organisms have shifted paradigms and allowed a new suite of more general questions in evolutionary ecology to be addressed. Processes as well as patterns of coadaptation and community assembly in multispecies systems, factors that promote mutualism stability, precision of adaptation, and subtle effects of

population size and structure on both sexual competition and molecular evolution are now being addressed using figs and wasps as model systems. Both from the perspective of general theoretical questions that can be addressed and from the perspective of the inherent interest of one of the most remarkable and important mutualisms in nature, figs and their associates continue to fascinate, instruct, and inspire.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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