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Foreword

Fig and fig wasp biology: A perspective from the East

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Abstract

The papers in this volume are the result of a meeting of fig and fig wasp biologists held in China, July 2006. Here we provide an overview of current themes in fig-fig wasp research and introduce the papers in this volume. Figs are pollinated by tiny, highly specific wasps whose larvae feed on a proportion of the flowers they pollinate. Other symbionts, including a diversity of non-pollinating wasps and vertebrate fruit eaters, exploit or otherwise depend on this obligate mutualistic interaction. Recently it was found that a substantial number of fig species harbour more than one species of pollinating wasp. This has lead to renewed interest in the question of specificity and its co-evolutionary implications. There has also been a substantial increase in the interest in fig and fig wasp biology in Asia, not least in China where our meeting was held. Directly following from this is an increased interest in dioecious figs, which are predominantly Asian. Dioecious figs offer a very different perspective on the stability of the fig-fig pollinator interaction to the better studied monoecious figs. They have also radiated into a remarkable diversity of ecological niches and, therefore, promise to reveal how fig-fig wasp interactions have responded to a variety of different ecological conditions. The study of non-pollinating fig wasp communities, which are every bit as interesting as the pollinating wasps, has been hampered by difficulties in determining their life-histories. A number of the papers presented here pioneer new methods to address these difficulties, and hence promise to prise open this field. Fig and fig wasp biology appears on the cusp of rapid developments on a number of fronts, and hence fig-fig wasp biologists can look forward with excitement to the coming years.

Keywords: *Ficus*, Agaonidae, mutualism, pollination, parasitism, frugivory, herbivory

> *"There is genuine paradox and real poetry lurking in the fig, with subulties to exercise an enquiring mind and wonders to uplift an aesthetic one..... But the fig is only one out of millions that all have the same Darwinian grammar and logic – albeit the fig story is amongst the most satisfyingly intricate in evolution."*
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> Richard Dawkins, Climbing Mount Improbable (1996)

1. Introduction

Since the classic papers on *Ficus* pollination by Galil and Eisikowitch (1968a, 1968b) and on the evolution of male dimorphism in non-pollinating fig wasps by Hamilton (1979), fig-fig wasp biology has been recognised as a model system for the study of interactions and their evolution. There have been over 800 publications on the topic in the past 40 years, and the rate of production shows no signs of abating. For over 25 years now, sycophilous researchers have been holding an international symposium on fig and fig wasp biology at approximately five year intervals. These symposia have resulted in two previous collections of papers (Bronstein and McKey, 1989; Compton et al., 1996). Fifteen out of the 22 papers in this special issue were presented at the 7th International Symposium on Fig and Fig Wasp Biology, held at Xishuangbanna Tropical Botanic Gardens, Yunnan, China in July 2006. The remaining seven were papers that arose from discussions among the participants, and were submitted to us immediately following the meeting.

The fact that our meeting was held in China reflects a recent shift of attention among researchers towards Asian figs. In particular, this has both promoted and been promoted by a growth of interest in fig biology within

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China. Along with this move towards Asia comes a greater interest in dioecious figs. In Africa dioecious figs are much less diverse and they are entirely absent from the Neotropics (Jousselin et al., 2003). The ecology of dioecious figs differs from that of monoecious figs, which have received much more attention, in many respects (Harrison and Yamamura, 2003; Harrison and Shanahan, 2005). Ecologies also vary tremendously among and within lineages of dioecious figs. Therefore, a greater understanding of dioecious figs promises to reveal not only how fig-fig wasp interactions differ in this system from that in monoecious figs, but how plant ecology has determined different co-evolutionary trajectories. In contrast, many monoecious figs have much more comparable ecologies, especially the diverse hemi-epiphyte lineages. Presumably exploitation of the hemi-epiphytic habit and the strictures of the canopy environment, have constrained the ecology of these figs within relative narrow limits. The ubiquitous diversity of monoecious hemi-epiphytic figs in tropical forests and their parallel radiation in Africa, Asia, Australasia, and the Neotropics makes them an ideal model for comparative study, as several papers in this volume illustrate. The papers presented here also reflect increased interest in the biology of non-pollinating fig wasps and other fig associated insects. While these organisms are potentially every bit as interesting to the evolutionary biologist as the pollinating wasps (Kerdelhué et al., 2000; West et al., 1996), difficulties in understanding their basic biology and complex community ecology have hampered studies. Several of the papers in this volume present new methodological approaches that address these difficulties and promise to prise open this field.

2. Why Figs are Interesting

Figs and fig wasps are scientifically interesting, not to mention culturally and aesthetically, for a great variety of reasons. Fundamental to these, however, are that figs (*Ficus* spp.) (1) possess a highly conserved pollination system, involving a highly specific seed predator-pollinator mutualism (Cook and Rasplus, 2003; Galil and Eisikowitch, 1968a), (2) support, often diverse, communities of non-pollinating wasps comprising competitors, parasites, and hyper-parasites of the pollinating wasps (Kerdelhué et al., 2000; West et al., 1996), (3) are essential resources in tropical forests for vertebrate fruit eaters (Shanahan et al., 2001), and (4) are pan-tropically distributed, globally diverse (≈750 spp.) (Berg, 2003), and form exceptionally species-rich local assemblages (Harrison, 2005). A further essential point is that of the countability of the contents of a fig inflorescence. This enables precise assessment of the resources available, sex allocation, and impacts of different symbionts on either fig or fig wasp reproductive success (Cook et al., 2004; Herre, 1989; Kjellberg et al., 2001; Nefdt and Compton, 1996; West and Herre, 1994). Together these factors make figs an ideal model system for exploring the comparative biology, behavioural ecology, and evolutionary ecology of a diversity of interactions.

3. A Background to Fig and Fig Wasp Biology

Ever since those classic papers by Galil and Eisikowitch the evolutionary ecology of the interactions between figs and their pollinators has been a source of scientific inspiration (Cook and Rasplus, 2003). Figs possess a closed, urn-shaped inflorescence lined with tiny flowers. The highly specific pollinating wasps enter through a narrow bract-filled passage, also called the ostiole. Once inside, they pollinate the tiny uniovular flowers, and simultaneously attempt to lay eggs in some of them. Fertilised flowers missed by the wasps develop into seeds. Ovules that receive an egg, however, develop into a gall, and the wasp larva feeds on the gall tissue. In a monoecious fig both seeds and wasp larvae develop together in the same inflorescence. Each wasp larva, therefore, develops at the expense of a potential seed; a trade-off that creates a fundamental co-evolutionary conflict between fig and pollinator (Herre and West, 1997). In dioecious species, by contrast, the inflorescences on female plants only produce seeds, while those on male plants produce pollinators and pollen (Galil, 1973). Wasps that enter a female inflorescence fail to oviposit. Thus, the system depends on the fact that the pollinating wasps are deceived into entering female inflorescences and pollinating them.

As adults, the pollinators emerge from their galls and mate within the inflorescence. The females then disperse, carrying a load of pollen from their natal fig, and must locate a receptive inflorescence during their short adult life-span (1–3 days) to reproduce. In some monoecious fig species, the pollinators disperse substantial distances (>30 km) using wind above the canopy, because the densities of flowering individuals are very low (Harrison and Rasplus, 2006; Nason et al., 1998). In other species, particularly some dioecious figs, with more frequent fruiting dispersal is more local (Harrison and Rasplus, 2006). The pollinators locate receptive trees using volatile cues (Grison et al., 2002b; Ware et al., 1993). One consequence of their unique pollination system is that figs must flower year-round at the population level. Any cessation of flowering that was longer than the lifespan of the pollinators would lead to their extinction, and thus quite probably to the extinction of the fig.

A taxonomically varied group of non-pollinating fig wasps and some other insects also exploit the fig inflorescence (Compton and Disney, 1991; Harry et al., 1996; Kerdelhué et al., 2000; West et al., 1996). These include gallers, parasites, and hyperparasites, most of which also occupy fig ovules. A majority of these species lay eggs by inserting their ovipositor through the wall of the inflorescence, although some gallers enter the inflorescence at the same time as the pollinator. Lest they be overlooked, we should add here that all these fig insects posses various internal symbionts, including for example parasitic nematodes (Herre, 1995) and *Wolbachia* (Shoemaker et al., 2002).

In a monoecious fig, 1–2 days after the wasps have departed the inflorescence ripens into a fig fruit. In dioecious figs, the female inflorescences, which do not support fig wasps, ripen directly at maturity. Globally over 1200 vertebrate species have been recorded feeding on figs, and they have been recognised as critically important resources for wildlife in many different places (Shanahan et al., 2001). Undoubtedly, this is largely due to the fact that fig fruit are available when other more seasonal fruit are scarce.

Globally there are approximately 750 fig species, which have been divided among six subgenera and 19 sections (Berg and Corner, 2005). However, most of the subgenera do not correspond to monophyletic lineages (Rønsted et al., this volume), and hence we do not consider them useful. The sections, on the other hand, correspond reasonably well with our current understanding of the evolutionary relationships, and can be defined primarily on the basis of plant habit and biogeography (Jousselin et al., 2003). In addition to their diversity at global and regional scales, it has also been noted that figs form exceptional diverse local assemblages (Harrison, 2005). In the Neotropics and Africa this is primarily due to the monoecious hemi-epiphytic figs. These figs are also diverse in the Asia-Pacific region, but here they are accompanied by several species-rich lineages of dioecious figs. The most diverse assemblage of species currently known is from NW Borneo where over 80 species have been recorded in a single habitat (Harrison, unpublished data).

4. Overview to the Papers in this Issue

This special issue is divided into four sections dealing with fig-fig pollinator interactions, phylogeny and evolution of figs and fig pollinators, fig phenology, and the biology of fig associated insects. To a large extent, of course, these are arbitrary categorisations. Fig phenology, for example, is important to both fig-fig pollinator interactions and the community ecology of non-pollinating wasps, while co-evolutionary processes obviously cannot be understood except in the light of the evolutionary relationships among species. However, these divisions made some sense to us at the time.

Fig-fig pollinator interactions

A few years back, it seemed as if we knew more-or-less how the fig-fig pollinator interaction worked, and one-to-one specificity of pollinator with fig host was the accepted paradigm. Then came the realisation that in a significant number of instances there were in fact two or more pollinator species per fig host (Kerdelhué et al., 1999; Lopez-Vaamonde et al., 2002; Molbo et al., 2003). Previously, exceptions to the one-to-one rule had been recorded (Rasplus, 1994). Indeed, over 40 years ago Wiebes wrote, "The fact is now unambiguously established, that more than one species of Agaonidae can reproduce in the receptacles of one fig…..I feel this conclusion, although it does not affect the general hypothesis of host specificity, should warn against too strict appliance of the principle in specific instances" (Wiebes, 1966). Clearly, however, this advice was not heeded. In the studies reported so far around 30–60% of the monoecious fig species studied harboured more than one pollinator (Kerdelhué et al., 1999; Lopez-Vaamonde et al., 2002; Molbo et al., 2003). However, a new study of dioecious figs in New Guinea found higher rates of specificity (Silvieus et al., in press). Obviously, patterns of host-specificity vary. Studies have to be extended to other geographical areas and across a wider taxonomic and ecological sample before general conclusions can be made. It also should be borne in mind that even in the studies reported so far 40–70% of species were species-specific. The fig-fig wasp interaction is still by far the most specific pollination system known (Harrison, 2007). It has just become a whole lot more interesting than perfect species-specificity would allow.

The presence of multiple pollinator species on a host upsets our former understanding of the stability of the fig-fig wasp interaction. With three or more players the number of potential co-evolutionary endpoints expands exponentially. In their paper Peng et al. describe a situation in *F. altissima* in which one of the two pollinators is a cuckoo; a non-pollinating "pollinator" that coexists alongside a legitimate pollinator. Moreover, morphological evidence suggests that it may have evolved from the legitimate pollinator. This is in contrast to a similar case reported from Africa in which the cuckoo had apparently colonised from a different, now extinct, species of fig (Kerdelhué et al., 1999).

In dioecious figs, pollinators that enter a female inflorescence fail to reproduce. The stability of the fig-fig wasp interaction in this system therefore depends on the fact that the pollinators cannot distinguish female inflorescences, and that once inside they pollinate the flowers. It has been known for some time that receptive figs release volatiles to attract pollinators (Grison et al., 2002b; Ware et al., 1993). Profitt et al., through a detailed study of *F. hispida*, show that there is chemical mimicry between male and female figs at the time of receptivity, but that this breaks down after the inflorescences have been pollinated. Raja et al. further show that pollination is achieved, because the pollinators exhibit the same behaviour in a female inflorescence as would have been appropriate had they entered a male inflorescence. Finally, Yanowit et al. demonstrate that there is selection in a male inflorescence for the behaviours associated with active pollination. Experimentally produced 'pollen-free' wasps produced lower numbers of offspring and unpollinated inflorescences were more prone to selective abortion.

Ficus pumila L. is a dioecious climbing fig commonly planted in gardens throughout the tropics. The fruits of one variety, *F. pumila* var. *awkeotsang*, are commonly eaten as a snack in south China, where it is indigenous. In their attempts to cultivate this variety, Chen et al. (a) found that, although there were wild populations of the same variety just 35 km away and of another variety next to the garden, initially there was complete pollination failure. Further experiments showed that the two varieties were reproductively isolated, and pollination was only achieved when the correct pollinators were introduced. Also working with *F. pumila*, Chen et al. (b) found that while there was greater genetic divergence in island populations, compared to the nearby mainland, overall genetic diversity was similar. Thus, although island populations may be experiencing some genetic isolation, they are sufficiently large to maintain similar levels of heterozygosity. This is in accordance with a previous study (Zavodna et al., 2005) finding similar genetic diversity in Krakatau archipelago and mainland populations of fig wasps. Together, these studies suggest that pollen dispersal maybe naturally limited to small local populations in some dioecious species.

Phylogeny and evolution of figs and fig wasps

Figs and fig wasps have been co-evolving for at least 60 million years, but possibly much longer (Rønsted et al., 2005; Zerega et al., 2005). Based on minimum fossil age constraints, radiation of the main extant lineages may have taken place from 30 to 60 million years ago (Rønsted et al., 2005), during the Eocene warm period when there was maximum isolation among the five principle rain forest blocks (Morley, 2000; Zerega et al., 2005). However, the fossil evidence is scant and considerably older dates are possible. Despite some notable progress (Jousselin et al., 2003; Rønsted et al., 2005; Weiblen, 2000), a well resolved molecular phylogeny for *Ficus* appears frustratingly elusive. In this volume, Rønsted et al. give the latest update on the progress. Using another nuclear gene (*G3pdh*) in combination with existing datasets for ITS and ETS they found increased support for some clades, but the branching order and some internal clades are still weakly supported. The global pollinator phylogeny is also still limited in terms of the number of taxa sampled and genes included (Jiang et al., 2006; Machado et al., 2001; Weiblen, 2001). However, the ongoing work on both figs and pollinators indicates that while we will find altered classifications, most fig clades will show correspondence with pollinator clades at the level of fig sections and above (Rønsted et al. and Rasplus et al. unpublished).

A consequence of multiple pollinator species, and the additional discovery that some are not host specific (Molbo et al., 2003), is that the co-evolutionary patterns within closely related clades potentially become much more complex (Machado et al., 2005). Jackson et al.'s phylogenetic analysis of Panamanian figs strongly suggests that there has been ancestral hybridisation. Moreover, when the fig and fig pollinator phylogenies are matched up their topologies show little congruence. So to what extent do phylogeny, or other factors, such as ecology (Harrison and Rasplus, 2006; Michaloud et al., 1996), similarity of volatile attractants (Grison et al., 2002a; Ware et al., 1993), or biogeography (Rasplus, 1994), determine host relationships?

Mirroring the findings reported from Panama, Su et al. found evidence of multiple pollinators on the same fig host and some pollinator species utilising different fig hosts in their study of Mexican fig wasps. Moreover, in combining their results with those from Panama they revealed at least one example of biogeography turn over of pollinators on the same fig host.

Fig phenology

A fig wasp can only lay eggs inside a fig inflorescence. The production of receptive inflorescences therefore determines the availability of reproductive opportunities for the wasps and, in turn, the production of adult wasps. Furthermore, the lifespan of an adult female wasp is very short (1–3 days). Thus, there is a very tight coupling between fig phenology and pollinator population dynamics. Any gap in the production of inflorescences for a period longer than the life-cycle of the wasp will lead to its extinction. Taking the comparative approach, Harrison found that flowering frequency in monoecious hemi-epiphytic figs was correlated to seed dispersal syndrome and pollinator dispersal behaviour. The results illustrate how an ecological trait of the plant is constrained through its interactions with different symbionts. Flowering asynchrony in figs extends the duration of sexual phases, increasing the opportunities for pollination (Bronstein and Patel, 1992). This may be advantageous in harsh environments, where flowering or wasp dispersal is limited by the conditions. This is exactly what Jia et al. (a) found in their study of two monoecious fig species in Australia. The species in the harsher environment flowered less frequently, but showed greater flowering asynchrony. One potential disadvantage of asynchronous flowering is the increased window of opportunity it affords non-pollinating wasps to lay their eggs (Cook and Power, 1996; Harrison and Yamamura, 2003). Lin et al. working in a strongly seasonal environment found a high degree of flowering asynchrony in their study species, but question the advantage given the predominance of non-pollinators in some inflorescences. Flowering asynchrony may also lead to self pollination if it extends to overlap between wasp producing and receptive phases. Some limited self-pollination may be advantageous to the male effort, if it helps maintain pollinator populations (Harrison and Yamamura, 2003). It is, therefore, not surprising that flowering asynchrony has been reported in several dioecious figs, where there is no penalty of inbreeding depression (Corlett, 1993; Harrison and Yamamura, 2003; Patel, 1996). Using the admirably experimental approach of bagging entire trees, Jia et al. (b) examined the hypothesis that a male dioecious fig could maintain its own pollinator population through flowering asynchrony. They found wasp populations survived up to three generations, but also showed that they were not stable in the long-term. It would be very interesting to take these phenological studies one step further, and examine the interaction between phenology, fig wasp community dynamics, and seed production over an extended period.

Community ecology of fig associated insects

A diverse and taxonomically varied group of non-pollinating wasps and some other insects also derive their livelihoods from the fig inflorescence (Compton and Disney, 1991; Harry et al., 1996; Kerdelhué et al., 2000; West et al., 1996). Most wasp species utilise the same ovules as the pollinators, and can be gallers (competitors), inquilines (gall parasites that kill the galler but feed mostly on gall tissue), parasites, or hyperparasites. Because these species all ultimately depend on the same resource – each individual exploits a single ovule, either by directly galling it or by replacing a gall occupant – their impacts on the production of seeds, pollinators, and one another can be precisely derived once the community structure is understood. However, difficulties in determining wasp life-histories have prevented this being achieved to date. The first four papers of the final section (Elias et al.; Wang and Zheng; Zhai et al.; and Yu et al.) describe the composition and organisation of different fig wasp communities. The first three papers show that species oviposit in a clear temporal sequence. Obviously, the feeding niche of a particular species must to some extent determine the timing of oviposition: A parasite cannot oviposit before its host. Historical constraint, as indicated by taxonomic status, must also to some extent determine feeding niche, although Elias et al. suggest that closely related species may sometimes occupy quite different niches. Zhai et al. also draw attention to a correlation between ovipositor length and the timing of oviposition for species feeding on the same resource. Later ovipositing species require a longer ovipositor, because elongation of the flower pedicles pushes the ovules away from the inflorescence wall. Finally, Yu et al. examine sex allocation and use the predictions of Local Mate Competition to assess oviposition strategies. They found the *Sycoscapter*, which if Tzeng et al.'s results can be generalised is a parasitoid, had highly female biased sex ratios indicating low foundress numbers per brood. In contrast, *Philotrypesis*, which is normally considered an inquiline, had slightly male biased broods indicating multi-foundress broods.

Perhaps the most interesting product of these studies is the diversity of methods the authors have pioneered to determine fig wasp life-histories. The next three papers in the section specifically present new methodological approaches. Pereira et al. show how sperm morphology can be used to solve the previously often intractable problem of determining which male belongs to which female. Meanwhile, Hsu et al. and Sergion-G and Sarmiento employ electron microscopy to reveal the details of larval development. Hsu et al.'s micrograph of a *Sycoscapter* larva feeding on the back of the *Ceratosolen* pollinator is the first direct observation of parasitism in a fig wasp. Similarly, Sergion-G and Sarmiento provide the first detailed documentation of larval development in a pollinating fig wasp. Together these studies provide a methodological framework for working out the structure of fig wasp communities.

A number of insects, including some flies and small wasps, that exploit fig inflorescences have much larger galls (Bouček, 1988; Compton and Disney, 1991; Roskam and Nadel, 1990). These usually either occupy ovules or gall the inner wall of the inflorescence. Although normally few in number, they can have a very substantial impact on seed and pollinator production, as Bai et al. demonstrate in their study of a gall midge on *F. benjamina* L.. Clearly, if we are to properly understand the structure and dynamics of fig wasp communities these insects need to be considered honorary fig wasps.

Other insects live externally on the fig inflorescences including ants and sap feeders, feed on or burrow through the inflorescence wall, or colonise the inflorescence after the fig wasps have departed (Basset and Novotny, 1999; Harry et al., 1996). From the perspective of fig-fig wasp interactions, ants are important as predators of fig wasps. They prey on all fig wasps, but wasps ovipositing through the wall of the inflorescence are particularly vulnerable. Some figs, therefore, apparently employ ants, through homopteran intermediaries, to control non-pollinating wasps (Cushman et al., 1998; Dejean et al., 1997). In the last paper of the section, Yang et al. explore the ecology of the entire community of insects, including fig wasps, predators (ants), sap feeders, pulp feeders, and decomposers, found on four sympatric fig species. Their focus is not on the intricacies of the fig-fig wasp interaction, but makes use of figs as a model for comparative study. Because of the ubiquity of figs in tropical forests, this approach could be usefully applied to a wide range of topics. Novotny and partners in Papua New

Guinea, for example, have made great progress in our understanding of herbivory and plant-herbivore interactions in tropical forests using figs as a model (Basset and Novotny, 1999; Novotny et al., 1999; Novotny et al., 2002).

Fig-fig eater interactions

One consequence of their unique pollination system is that fig fruit are available when other more seasonal fruit are scarce, and this makes them a vital resource for many fruit eating vertebrates in tropical forests (Shanahan et al., 2001). This is especially true of the large monoecious hemi-epiphytic figs, which attract diverse frugivore assemblages (Shanahan and Compton, 2001). Low densities of fruit trees, however, forces frugivores to range over a large area of forest.

In contrast, many dioecious figs produce smaller crops, which attract less diverse frugivore assemblages, but may be more locally dependable resources (Shanahan and Compton, 2001). Despite constraints in the structure of the fig inflorescence, figs also manage to package their fruit in a surprising diversity of ways (Shanahan et al., 2001). This is particularly true of dioecious figs which have the smallest (<0.4 cm) and largest (>12 cm) diameter figs, evidence the full gamut of natural fruit colours, can be soft throughout or hard on the outside and peel like an orange, and may be displayed among the leaves, along the branches or truck, on the ground, and even in the soil (Corner, 1988; Harrison and Shanahan, 2005). Even among monoecious hemi-epiphytic figs studies in Panama revealed two distinct syndromes; small red bird-dispersed figs and larger green bat-dispersed figs (Kalko et al., 1996). The latter evidenced a range of sizes with larger bats favouring larger figs. Reflecting co-evolution with an unrelated frugivore assemblage, monoecious hemi-epiphytic figs in Borneo were shown to have somewhat different fruit designs. Strictly bat-dispersed figs were still large and green but comprised only one species. Meanwhile, canopy bird-and-mammal (including bat) dispersed species were orange-red to black in colour and ranged from small to large in size (<1–>3 cm diameter). Larger species tended to be found higher in the canopy and were fed on by a separate sub-guild of fruit eaters, in particular the large hornbills (Shanahan and Compton, 2001).

No comparable study exists for Africa, but over the continent as a whole it was found that the diversity of fig species was the strongest determinant of frugivorous bird diversity, indicating the importance of figs even at such scales (Kissling et al., 2006).

It is something of a shame that nobody presented a paper on fig-frugivore interactions at the meeting in Xishuangbanna. Let us hope that this brief overview might serve to stimulate further studies on this very interesting topic.

5. Conclusions

Despite four decades and over 800 scientific publications since Galil and Eisikowitch (1968a), the fig-fig wasp system cannot be considered well understood. Recently held paradigms, such as the strict one-to-one species specificity of pollination, lie shattered. In addition to the pollinators, figs are host to several trophic layers of fig wasps, including gallers, parasites and parasitoids, and other insect assemblages. Most of which have received little attention. Moreover, despite the importance of figs to fruit eaters, there have been just two studies of community-wide fig-frugivore interactions. Compton et al. (1996) in their introduction to the last proceedings volume on fig-fig wasp biology paraphrased Janzen's (Janzen, 1979) title "How to be a fig" to "There are many ways to be a fig". There also many ways to be a fig wasp (Weiblen, 2002). And there are many, many more ways for figs, fig wasps and their associates, and fig eaters to interact.

Almost 20 years ago in the introduction to the first proceedings volume on fig-fig wasp biology, Bronstein and McKey stated that with over 750 pairs of interacting species figs and fig wasps are a model system for comparative biology (Bronstein and McKey, 1989). However, with such a large study system, we also have to recognise the diversity within the system. Recent studies on pollinator specificity have focused on the monoecious figs, whereas dioecious figs have largely been overlooked, although Weiblen and co-workers are shedding new light on sections *Sycocarpus*, *Sycomorus*, and *Adenosperma* (Silvieus et al., in press). At the same time, species limits of figs are somewhat uncertain and hundreds of fig pollinators still await formal description. However, the realisation that old rules are no longer valid, allows us to look with fresh eyes at figs and fig pollinators. We are also starting to establish methods for conducting good descriptive and comparative studies, particularly with respect to the non-pollinating fig wasp fauna. We are beginning to obtain the phylogenetic framework needed to evaluate the patterns and processes of evolution within the system. One cannot emphasize enough the need to have good taxonomy of both figs and figs wasps, so we can identify them and have some sort of consensus as to what a species is. DNA sequence variation may be a helpful tool in trying to define species limits. We also need to look at the community ecology of all the insects associated with a particular fig host, and across different fig species within the same forest, to understand the selective environment that has resulted in different co-evolutionary endpoints. Figs and their fig wasps remain a remarkable model system (perhaps we should say 'super-model' system) for studies of co-evolution. Figs are also ideal models for many other types of study, and they are of huge importance for the conservation of tropical and subtropical forests worldwide.

We hope the present collection of papers will show where the field stands today and be an inspiration for future research. Fig and fig wasp biology appears on the cusp of rapid developments on a number of fronts, and hence fig-fig wasp biologists can look forward with excitement to the coming years.

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