

## Maintenance of Specificity in an Isolated Fig

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### ABSTRACT

The obligate interaction between figs and their pollinating wasps is often cited as an extraordinary example of reciprocal species specificity and evolutionary cospeciation. However, recent studies have shown that breakdowns in one-to-one specificity are not rare (30–60% of species depending on the locality). Combined with evidence of hybridization in some species, this led researchers to propose that a better evolutionary model was one of groups of genetically well-defined pollinators coevolving with groups of frequently hybridizing figs. Nevertheless, these recent studies still indicate that a majority of fig species have one or more host-specific pollinator. The extent to which specificity barriers in these species are leaky will have important consequences for the evolutionary process in *Ficus*. At Lambir Hills N.P., Sarawak, a single individual of *Ficus acamptophylla* has become recently isolated from conspecifics through clearance of its specialized habitat, but adjacent forest has a diverse fig flora, including 16 species with congeneric pollinators. Thus, when this individual flowered I was able to investigate the maintenance of its specificity barriers in the absence of competition from the normal pollinator. Only 1 percent of inflorescences were entered by a single pollinator species, which had very low reproductive success, and no viable seeds were produced. Nonpollinating wasps also failed to reproduce in any of the inflorescences. These results indicate the maintenance of strict specificity barriers in this fig individual.

*Key words:* Agaonidae; coevolution; *Ficus*; host specificity; seed predator-pollinator.

MUTUALISMS ARE UBIQUITOUS IN NATURE. Their degree of specificity and long-term variability have important, and as yet poorly understood, consequences for the evolution and maintenance of biological diversity (Thompson 1994, Leigh 1999). Interactions between plants and their pollinators are usually unspecialized, highly variable from place to place, and from one flowering event to the next, and wasteful in terms of the proportion of ovules that receive pollen from a conspecific individual (Roubik *et al.* 2003). Obligate pollination mutualisms are rare, but evidence high levels of reciprocal specificity and diversity (Kawakita 2004 #2351; Pellmyr 1996 #445; Berg 2005 #2700). The interaction between figs (*Ficus*, Moraceae) and fig wasps (Agaoninae; Chalcidoidea) is perhaps the most specialized pollination mutualism known. The partnership is at least 60 Myr old (Ronsted 2005 #2595) and *Ficus* is one of the most diverse genera of dicotyledonous plants, both in terms of species richness and the breadth of ecological niches figs have come to occupy (Harrison 2005).

Fig wasps are seed predator-pollinators that enter the closed fig inflorescence to breed. As wasps search among the tiny flowers for suitable sites to lay their eggs, they disperse pollen carried from their natal fig. The wasp offspring develop inside galled ovules, each larva destroying a single potential seed. Other pollinated ovules develop into seeds in the normal way. A few weeks later, the wasp offspring emerge from their galls and mate within the inflorescence. The females then disperse, collecting (actively or passively) a load of pollen on the way out. They must find a receptive fig within their brief life span to reproduce. Each partner is thus mutually dependent on the other. Critically, the pattern of fig gene flow depends on the host specificity of their ovule-galling pollinators. Superficial sampling across a broad range of fig species led to a notion of one-to-one

matching between figs and their pollinators (Wiebes 1966, Ramirez 1974, Berg & Wiebes 1992), which in turn led to the adoption of cospeciation as the default model of coevolutionary divergence (Weiblen 2002, #1886; Cook 2003) #2461). Exceptions to the rule are, however, frequent (Rasplus 1994). Recent detailed studies based on substantial sampling have found that between approximately 30 percent and 60 percent of species, depending on the locality, are interacting with more than one partner (Kerdelhué *et al.* 1999, Lopez-Vaamonde *et al.* 2002, Molbo *et al.* 2003). Importantly, several instances in which two or more fig species share a common pollinator have been reported (Rasplus 1994, Lopez-Vaamonde *et al.* 2002, Molbo *et al.* 2003). Phylogenetic studies also indicate several clear instances of host switching, but provide little support for cospeciation (Machado *et al.* 2005). Based on these findings and evidence of introgression among a small community of figs in Panama, Machado *et al.* (2005) have suggested that a more appropriate evolutionary model is that of groups of genetically well-defined species of wasps coevolving with groups of genetically indistinct, frequently hybridizing, species of fig.

Nevertheless, even the more detailed recent studies find that the majority of fig species are interacting with a few host-specific pollinators. Clearly, the degree to which the specificity barriers in these species are leaky will strongly influence the evolutionary dynamics of the interaction. There are some reports of breakdowns in specificity in introduced or colonizing fig species (Ramirez 1994, #125; Compton, 1990 #543, Parrish 2003 #2091). Conversely, several fig species transported around the world by the horticultural trade were not pollinated until their own pollinators were accidentally introduced (Ramirez & Montero 1988, Nadel *et al.* 1992, McPherson 2005, Corlett 2006). In one interesting case in South Africa a *Ficus lutea* Vahl tree planted roughly 500 km outside its natural range was visited by two local pollinator species, and moreover the propensity to produce viable seeds increased with relatedness

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to the normal pollinator (Ware & Compton 1992). However, introducing a species outside its natural range may bypass important specificity barriers, because the interacting species have no coevolutionary history. This is made clear by the fact that the sacred Pipal tree (*Ficus religiosa* L.) from India has hybridized with two fig species in Florida that are completely unrelated to either the Pipal or one another (Ramirez 1994). Unfortunately, investigating the leakiness of specificity barriers within the natural range of a species is difficult. It involves sifting through a very large number of inflorescences (and identifying all the pollinators) to find the occasional one pollinated by a different wasp species.

At Lambir Hills National Park (Lambir; 4°20'N 113°50'E, 150–250 m asl), Sarawak, Malaysia, one fig individual has become very isolated from conspecifics through recent clearance of its specialized habitat although the adjacent forest has a diverse fig flora including several closely related species. The situation is analogous to the *F. lutea* tree studied in South Africa, but within the natural range of the species. When this individual flowered I was able to investigate the maintenance of specificity in the absence of the normal pollinator.

*Ficus acamptophylla* Miq. is a monoecious hemi-epiphytic fig (subgenus *Urostigma*) pollinated by *Waterstoniella obvenata* Wiebes. It has an unusual vine-like growth form and grows along streams in freshwater swamp forests, with its branches hanging down over the water. A large peat swamp forest formerly surrounded Lambir on roughly two sides, but has been cleared for timber, oil palm plantations, and rice cultivation over the past two decades (Ashton 2005). A single *F. acamptophylla* individual remains by a pond near the laboratory buildings at Lambir. The park is otherwise hilly and, therefore, does not support habitat suitable to this species. This *F. acamptophylla* individual is now isolated from mature swamp forest with conspecifics by approximately 20 km, although other remnant individuals may exist. Some fig pollinators are known to disperse substantial distances (Nason 1998) #960). At Lambir it was estimated that some fig wasps must be arriving from forests 30 km or more away (Harrison 2003 #2410). Long-distance separation from conspecifics does not, therefore, necessarily mean genetic isolation in figs. However, during these studies of pollinator dispersal at Lambir *W. obvenata* was not collected, suggesting the

TABLE 1. The contents of 313 inflorescences of an isolated individual of *Ficus acamptophylla* at Lambir.

	No. of inflorescences	No. of wasp offspring (range)	No. of viable seeds (range)
Not entered	305	0	0
Pollinator entered	3	4–6	0
Nonpollinator entered	5	0	0

*F. acamptophylla* individual at Lambir is, indeed, substantially isolated from conspecifics.

Seventy-nine other *Ficus* species occur at Lambir, including the probable sister species (*F. paracamptophylla* Corner) and a further 16 species pollinated by *Waterstoniella* wasps (Harrison & Shanahan 2005). Seventeen *Waterstoniella* species have been caught above the canopy at Lambir over a few days of sampling (Harrison 2003 #2410). In late December 2005 the *F. acamptophylla* individual at Lambir produced a crop of several thousand inflorescences. The crop apparently developed normally and matured toward the end of January 2006 producing ripe figs that were fed on by a range of frugivorous birds and squirrels.

I sampled inflorescences to collect the wasps, but found that the majority had not been entered by pollinating wasps or other nonpollinating fig wasps. I dissected 313 inflorescences (all the inflorescences that were easily accessible) under a binocular microscope checking the ostiole bracts for evidence (wings or antenna parts) that wasps had entered, and thoroughly searching the interior for foundress wasps, galls, or viable seeds. Over 97 percent of these inflorescences had not been entered at all, 1.6 percent had been entered by a nonpollinator, and just 1.0 percent (4 inflorescences) had been entered by a pollinator (Table 1). I also did not find any galls of nonpollinating species that lay their eggs through the wall of the inflorescence, which are common on related fig species at Lambir. All three inflorescences were entered by the same species of pollinator (possibly *Waterstoniella borneana* Wiebes, a pollinator reported from *F. binmendiikii* Miq., or a species closely related to it). Few mature wasp offspring (four, four, and six, respectively) and no viable seeds were, however, produced (they were all hollow) (Table 1). There was also no evidence of pollinator galls that had failed to develop. Five inflorescences were entered by a *Diaziella* nonpollinator (possibly *D. falcata* Wiebes; Pteromalidae) and, although some nonpollinators have been shown to occasionally pollinate (Jousselin *et al.* 2001), neither viable seeds nor galls were found.

The specificity barriers in this fig would appear to be very strict. Despite the diverse fauna of pollinators that potentially could have entered the inflorescences, only one species did so. It colonized a very small proportion of inflorescences and had low reproductive success. Moreover, no viable seeds were produced. Under normal circumstances competition from the usual pollinator may be expected to limit nonspecialist pollinator success even further, suggesting even higher pollinator specificity. The fact that another pollinator species entered at all demonstrates that the barriers are

not perfect, and over evolutionary timescales even such low levels of specificity-breakdown might be important. It is also interesting that nonpollinators failed to colonize the inflorescences. A diversity of galler species lay their eggs through the walls of fig inflorescences (West & Herre 1994, Kerdelhué *et al.* 2000), which would not apparently demand such strict species-specific adaptation (Hill 1967). A final point of interest is that nonpollinated inflorescences were retained on the twigs. Usually in the absence of pollination inflorescences are abscised, which is often suggested as a mechanism whereby figs police the mutualism. Some wasps can induce their hosts to retain inflorescences without pollination (Weiblen *et al.* 2001, Jouselin *et al.* 2003). However, in this case inflorescences that were neither pollinated nor contained any galls were retained.

Throughout the tropics, figs form very species-rich assemblages, and within communities a fine-scale niche differentiation in terms of microhabitats, seed dispersal syndromes, and reproductive traits is evident (Harrison 2005). Clearly, the maintenance of high sympatric species diversity with fine ecological specialization must depend on relatively strict genetic isolation among species. Therefore, we should not be surprised to find examples of high pollinator specificity, as reported here. Recent studies based on substantial sampling (Kerdelhué *et al.* 1999, Lopez-Vaamonde *et al.* 2002, Molbo *et al.* 2003), combined with observations such as those reported here, indicate that the great majority of fig pollinators are highly specific. The extent to which hybridization contributes to the evolutionary process in *Ficus* must thus depend on how membership of the minority of species that share pollinators varies as the composition of fig assemblages changes from place to place and over time.

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