

The evolution of dioecy among Ficus (Moraceae): an alternative hypothesis involving non-pollinating fig wasp pressure on the fig–pollinator mutualism

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In *Ficus* (Moraceae), about half of the species are monoecious and half are (gyno)dioecious. With a few exceptions (Kerdelhué et al. 1996, Rasplus in press), each is specifically associated with one single pollinating chalcid wasp (Chalcidoidea: Agaonidae: Agaoninae), which in turn only breeds on that fig species (Wiebes 1963). In monoecious *Ficus* species, the figs (or syconia) produced by all the trees contain both male and female flowers; the latter are set out in three or more ovary layers and have styles of various lengths. When the pollen-loaded female wasp enters the fig cavity, it lays eggs through the styles in the upper ovary layer (i.e. in the flowers with styles that are short enough for the ovipositor to reach the ovule) and pollinates the deepest flowers (Galil and Eisikowitch 1971). Basically, the outermost ovary layer will turn into seeds, whereas the inner ones will be transformed into galls and shelter pollinator larvae. By the time the wasp offspring emerges from the galls in the fig cavity, the male flowers reach maturity. When escaping from the syconium, the female wasps will bring pollen out, up to a young receptive fig.

In dioecious *Ficus*, half of the trees bear figs that only contain one or two layers of long-styled female flowers. When the female wasp enters the cavity, it can pollinate but is not able to lay any egg. These figs will produce seeds, but no pollinators or pollen grains: such trees are functionally 'female' (Berg 1984). The rest of the trees produce figs with one or two layers of short-styled flowers, as well as male flowers. The wasp will thus be able to lay eggs in all ovaries, and its offspring will disseminate the pollen. These figs will produce pollen and pollinator wasps, but almost no seeds; such trees are functionally 'male'.

In addition to its mutualistic partner, each *Ficus* species is associated with a great diversity of non-pollinating chalcid wasps (Hamilton 1979, Janzen 1979, Bronstein 1991, Compton and Van Noort 1992, Hawkins and Compton 1992, Bouček 1993), mostly belonging, like the pollinator, to the Agaonidae family (Bouček 1988). These wasps may be numerous (up to thirty species: Compton and Hawkins 1992), and mostly breed in the fig flowers. Some are gall-makers, and oviposit in vacant ovaries; they lay eggs either from the fig cavity at the same time as the pollinator, or from outside the fig thanks to a long ovipositor. Most of these oviposit after pollination has occurred, and regardless of the oviposition place, they were proved to similarly lay eggs in the most internal ovary layers (West and Herre 1994, Kerdelhué and Rasplus 1996). Kerdelhué and Rasplus (1996) have suggested that they are unable to oviposit in pollinated ovaries. The other species of non-pollinating fig wasps lay eggs in previously gall-transformed ovaries that already shelter a larva. These insects are either parasitoids (their larva directly feeds on the developing larva of another species) or inquilines (their larva feeds on the gall plant tissue; if the first larva starves to death, the inquiline is functionally parasite; if not, it acts as a commensal).

Among dioecious species, *Ficus carica* is one of the best studied (Valdeyron and Lloyd 1979). Its particular fruiting phenology was proved to stabilize the *Ficus*–*Blastophaga* symbiosis in the south of France. This has led to dioecy being considered as an adaptation to seasonal climates (Kjellberg et al. 1987). Although plausible, this hypothesis is limited by the existence of dioecious figs in tropical environments (Patel et al.

1993). Therefore, we here propose an alternative evolutionary scenario in which dioecy would have appeared under the selective pressure of non-pollinating fig wasps on the mutualism. Our reflexion is based on original data and reviews of both monoecious and dioecious *Ficus* species.

Hypothesis

Unlike the figs of dioecious *Ficus* which contain 1 or 2 ovary layers and present perfect heterostyly, those of monoecious *Ficus* contain 3 or 4 ovary layers and present imperfect heterostyly (Verkerke 1989). Our hypothesis is illustrated on the basis of *Ficus sur*, a monoecious species (Kerdelhué and Rasplus 1996). Schematically (Fig. 1a), the inner short-styled flower ovaries are mostly occupied by larvae of insects that oviposit from the fig cavity, that is, *Ceratosolen* (pollinator) and *Sycophaga* (gall-maker) and by their para-

sites (i.e. parasitoids or inquilines). All these fig wasps also develop in the second ovary layer, but here some other gall-makers are also found, which lay eggs from the outside (*Apocryptophagus*). The third layer produces a few seeds, and shelters mainly *Apocryptophagus* and, more rarely, some remote *Sycophaga* individuals. Outermost is the seed layer, yet some *Sycophaga* and a few *Apocryptophagus* can occasionally be found. If the non-pollinating wasps are very numerous, the medium layers will be occupied entirely by exploiters (Fig. 1b), and the flowers involved will serve neither the female nor the male function of the *Ficus*. This probably represents a high cost for the fig tree. In such a case, an individual tree producing fewer flowers, but whose ovaries are out of reach of the non-pollinating wasps, should be favoured within a monoecious fig tree population. This may occur if the medium ovary layers, that is, the non-pollinating fig wasp oviposition sites, disappear, and if the fig only produces either internal or external ovary layers (Fig. 1c).

Basically, in a stable monoecious fig tree population, the ratio of short- and long-styled flowers results from two selective pressures. First is the maximum flower production; the development of a great number of flowers within a syconium results in competition for space. This leads to ovary stratification, and hence to the production of numerous flowers of various style lengths (Verkerke 1989). Second is the conflict between the female (seed production) and male (pollen plus pollen-vector production) functions of the tree. On the one hand, drive to produce longer and longer styled flowers in increasing number (i.e. to produce 'female' figs) might be countered because the pollen carriers produced by short-styled flowers will be critically reduced; similarly, drive to produce smaller and smaller styled flowers in increasing number (i.e. to produce 'male' figs) will be countered because seed production will dramatically decline. On the other hand, the production of a maximum number of flowers per fig will ineluctably lead to more developed medium flower layers, which are a reproductive niche for non-pollinating fig wasps.

As long as the costs due to these non-pollinating wasps do not exceed a certain threshold, the evolutionarily stable strategy for fig trees will be monoecy. Beyond that threshold, any mutation inducing a higher proportion of long-styled (or of short-styled) flowers in the figs of a given tree, and a reduction of the ovary layers, will be favoured and gradually invade the population via the extra seeds produced (or extra pollen dissemination). The first evolutionary step would be a polymorphic population of monoecious trees producing figs with higher proportions of either long-styled or short-styled flowers, which will gradually evolve towards a real dioecious species.

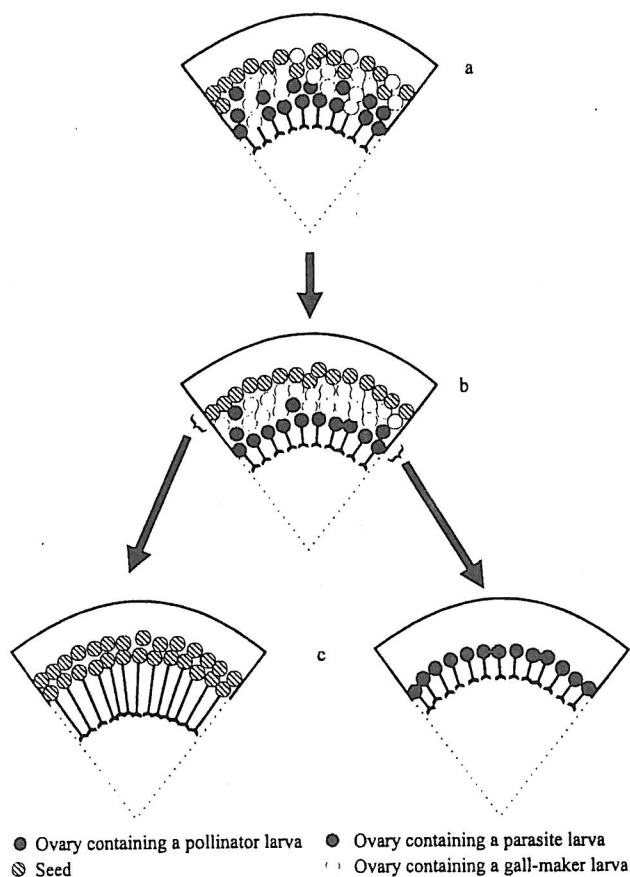


Fig. 1. Schematic representation of the evolution towards dioecy under non-pollinating fig wasp pressures. The assumption is that in highly exploited monoecious *Ficus* species (a), the non-pollinating species tend to entirely use the medium ovary layers at the expense of the pollinators, while the external seed layer remains untouched (b). Evolution towards dioecy can then occur since the separation of long- and short-styled flowers in different fig trees efficiently limits the costs due to the non-pollinating fig wasps (c).

Table 1. Number of parasites and gall-makers occurring on 9 dioecious and 10 monoecious fig species, from 4 and 5 *Ficus* sections respectively.

Dioecious <i>Ficus</i> species				Monoecious <i>Ficus</i> species			
<i>Ficus</i> species	Section (subgenus)	Number of parasites	Number of gall-makers	<i>Ficus</i> species	Section (subgenus)	Number of parasites	Number of gall-makers
<i>hirta</i>	<i>Ficus</i>	3	0	<i>benghalensis</i>	<i>Conosycea</i>	13	5
<i>carica</i>	<i>Ficus</i>	2	0	<i>aurea</i>	<i>Americana</i>	4	6
<i>nota</i>	<i>Sycocarpus</i>	3	1	<i>drupacea</i>	<i>Conosycea</i>	3	3
<i>exasperata</i>	<i>Sycidium</i>	2	0	<i>macrophylla</i>	<i>Malvanthera</i>	4	2
<i>hispidoides</i>	<i>Sycocarpus</i>	3	1	<i>microcarpa</i>	<i>Conosycea</i>	2	9
<i>semicordata</i>	<i>Sycidium</i>	2	1	<i>pertusa</i>	<i>Americana</i>	1	3
<i>variegata</i>	<i>Neomorphe</i>	2	1	<i>thonningii</i>	<i>Galaglychia</i>	18	9
<i>asperifolia</i>	<i>Sycidium</i>	2	0	<i>sycomorus</i>	<i>Sycomorus</i>	4	6
<i>fistulosa</i>	<i>Sycocarpus</i>	2	0	<i>ovata</i>	<i>Galaglychia</i>	12	6
				<i>sur</i>	<i>Sycomorus</i>	6	6

Predictions from the hypothesis

Assuming our scenario of appearance of dioecy is valid, two predictions can be made. First, we can expect to find much fewer non-pollinating fig wasp species on dioecious than on monoecious fig species; second, the chalcid fauna occurring on dioecious fig trees should be mainly composed of pollinator parasites. Both predictions are fully supported by an analysis we conducted on 10 monoecious and 9 dioecious well sampled fig species, chosen among 9 *Ficus* sections and subgenera. The data are presented in Table 1. Monoecious *Ficus* were proved to be associated with a significantly larger number of non-pollinating wasps than dioecious *Ficus* (One-way ANOVA: $F(1,17) = 15.99$, $p < 0.01$: see Fig. 2). Consistent also with the predictions, the non-pollinating chalcid wasps associated with dioecious species are mainly pollinator parasitoids or inquilines. It should also be stressed that these wasps never occur in female trees, and the rare gall-makers that exploit male

figs are all early-ovipositing species. No gall-makers that lay eggs through the fig wall after pollination have ever been found so far in dioecious figs. Finally, in support of our assumption, only half of the non-pollinating fig wasps occurring on monoecious *Ficus* are parasites, all the others being gall-makers (Fig. 3).

Kjellberg et al. (1987) hypothesized that dioecy would have appeared as an adaptation to seasonal climates. If so, dioecious *Ficus* should be found exclusively under temperate climates, and should invariably exhibit the sexual differentiation of reproductive phenology observed in the *Ficus carica*–*Blastophaga psenes* mutualism. However, many dioecious fig species are found under tropical climates; in particular, *F. fistulosa* (Corlett 1987) and *F. hispida* (Patel et al. 1993) were proved to exhibit flowering asynchrony in non-seasonal environments, like monoecious species. Therefore, we consider that dioecy appeared under non-pollinating fig wasp pressure in the tropics, and only secondarily allowed these *Ficus* species to develop under seasonal climates. The colonization of temperate environments would thus be a consequence (rather than a cause) of the appearance of dioecy.

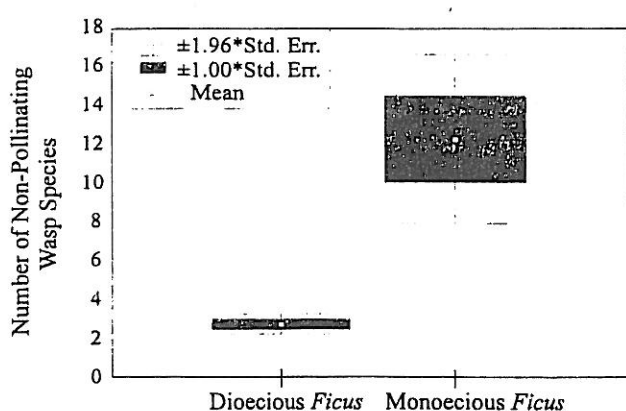


Fig. 2. Mean number of non-pollinating wasp species occurring on monoecious and dioecious *Ficus*. A sample of 10 monoecious and 9 dioecious *Ficus* species was studied: Monoecious: *F. aurea*; *F. benghalensis*; *F. drupacea*; *F. macrophylla*; *F. microcarpa*; *F. pertusa*; *F. thonningii*; *F. ovata*; *F. sur*; *F. sycomorus*. Dioecious: *F. asperifolia*; *F. carica*; *F. exasperata*; *F. fistulosa*; *F. hirta*; *F. hispidoides*; *F. nota*; *F. semicordata*; *F. variegata*.

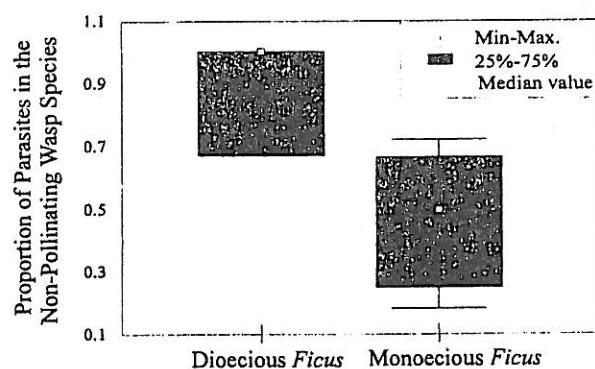


Fig. 3. Proportion of parasitoids and inquilines within the non-pollinating fig wasp faunas of 10 monoecious and 9 dioecious *Ficus* species. The 25%–75% limits correspond to the numbers of species below and above which 25% of the faunas are found. The *Ficus* species studied are the same as in Fig. 1.

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