

Pollination and parasitism in functionally dioecious figs

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Fig wasps (Agaonidae: Hymenoptera) are seed predators and their interactions with *Ficus* species (Moraceae) range from mutualism to parasitism. Recently, considerable attention has been paid to conflicts of interest between the mutualists and how they are resolved in monoecious fig species. However, despite the fact that different conflicts can arise, little is known about the factors that influence the persistence of the mutualism in functionally dioecious *Ficus*. We studied the fig pollinator mutualism in 14 functionally dioecious fig species and one monoecious species from tropical lowland rainforests near Madang, Papua New Guinea. Observations and experiments suggest that (i) pollinating wasps are monophagous and attracted to a particular host species; (ii) pollinating and non-pollinating wasps are equally attracted to gall (male) figs and seed (female) figs in functionally dioecious species; (iii) differing style lengths between gall figs and seed figs may explain why pollinators do not develop in the latter; (iv) negative density dependence may stabilize the interaction between pollinating wasps and their parasitoids; and (v) seed figs may reduce the search efficiency of non-pollinators. This increased pollinator production without a corresponding decrease in seed production could provide an advantage for dioecy in conditions where pollinators are limiting.

Keywords: Agaonidae; *Ficus*; mutualism; parasitism; pollination

1. INTRODUCTION

Mutualisms involving pollinating seed predators and host plants are generally characterized by a conflict involving the allocation of plant resources (Anstett *et al.* 1996; Herre *et al.* 1999). Conflict can be measured by comparing the numbers of seeds and pollinators produced in host plants that donate a fraction of their seeds as food for pollinator larvae in exchange for pollination services (Herre & West 1997). In particular, the consumption of too many seeds by pollinator larvae could transform a mutualistic relationship into a parasitic one, perhaps even resulting in extinction.

The best-studied example of this form of conflict is that between figs (*Ficus* species, Moraceae) and their pollinating wasps (Agaoninae: Hymenoptera) (reviewed in Herre 1989, 1996; Herre & West 1997). Female pollinators lay eggs by inserting their ovipositors into the styles of fig flowers. Eggs deposited between the integument and nucellus of fig ovules develop into larvae that feed on endosperm (Grover & Chopra 1971). Individual pollinators would benefit from laying eggs in all ovules, but the evolutionary spread of such a strategy would preclude seed production and eventually drive the host population to extinction. Previous work has identified factors that can stabilize the seed–pollinator conflict in monoecious fig species (West & Herre 1996; Nefdt & Compton 1996) and the aim of this paper is to examine hypotheses purporting to explain how conflict is resolved in functionally dioecious figs.

Approximately half of the world's 750 *Ficus* species are functionally dioecious, bearing 'male' and 'female' figs on separate plants, which are known as gall figs and seed figs

(Berg 1989; Weiblen 2000). Female wasps pollinate and attempt to lay eggs in both types of figs but their offspring only develop in gall figs, providing a proximate resolution of the seed–pollinator conflict (King 1887; Galil & Eisikowich 1968a). Gall figs are functionally male because they foster the wasp larvae that disperse fig pollen as adults (Weiblen *et al.* 1995). Seed figs are functionally female and produce viable seeds because the styles are too long for pollinator ovipositors to reach the ovules, whereas gall fig styles are short (Ganeshaiah *et al.* 1995). In sum, fig ovules are allocated to each generation of seeds and wasps in a predictable fashion.

However, functional dioecy creates a conflict between figs and pollinators that is not seen in monoecious species. Any pollinator that visits a seed fig is entombed and fails to reproduce, whereas the pollinators of gall figs achieve fitness. As a result, it would be advantageous for a pollinator to avoid seed figs, but this has not been observed (Patel *et al.* 1995). Grafen & Godfray (1991) suggested that pollinators are unable to differentiate between seed and gall figs due to selection for the two types of figs to resemble each other, a process they termed 'vicarious selection', but to date few data have been available to evaluate this hypothesis.

The persistence of the pollination mutualism in functionally dioecious figs may also be impacted on by the stability of host–parasitoid interactions, as in the case of monoecious figs (West & Herre 1994; West *et al.* 1996). Non-pollinating parasitoids and gallers are species-rich components of fig wasp assemblages, having negative impacts on the mutualism through predation of pollinator larvae and through competition with pollinators for seed resources (Compton *et al.* 1994; West & Herre 1994; West *et al.* 1996). If host–parasitoid interactions are not stable, theory predicts ever-increasing population cycles leading

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to the eventual extinction of the parasitoid and its host and, therefore, to the extinction of the mutualism. West *et al.* (1996) suggested that spatial heterogeneity in the risk of parasitism may stabilize host–parasitoid population dynamics in accord with predictions of host–parasitoid theory (May 1978; Pacala *et al.* 1990). Kerdelhue & Rasplus (1996) suggested that functional dioecy may limit the incidence of parasitism because seed and gall figs have fewer ovary layers compared with monoecious figs. Assuming that the coexistence of parasites is mediated by the partitioning of resources according to ovary position (Cook & Power 1996), the absence of multiple ovary layers is hypothesized to have allowed pollinators to exclude non-pollinators competitively, thereby resulting in lower species richness and abundance in functionally dioecious figs (Kerdelhue & Rasplus 1996).

Here we use a combination of observational and experimental approaches to assess whether the hypotheses presented above apply to functionally dioecious figs in Papua New Guinea. Specifically, (i) we examine pollinator specificity and document that style length differences in seed and gall figs provide a proximate resolution of the seed–pollinator conflict in *Ficus hispidooides*, (ii) we find that both pollinators and non-pollinators do not differentiate between seed and gall figs of this species, supporting the vicarious selection hypothesis, (iii) we demonstrate levels of heterogeneity in the rate of fig parasitism in *Ficus trachypison* that are sufficient to stabilize host–parasitoid dynamics, and, finally, (iv) we observe that non-pollinators have a less negative impact on functionally dioecious species than on a sympatric monoecious species. The inability of fig wasps to differentiate seed figs from gall figs suggests that seed figs act as ecological sinks, limiting the search efficiency of non-pollinators. This provides an alternative explanation for the lower species richness and abundance of non-pollinators in functionally dioecious *Ficus*.

2. MATERIAL AND METHODS

(a) Study area

The study area was located in the Madang district of Papua New Guinea in moderately disturbed lowland rainforest and coastal forest at 0–400 m above sea level. Collections and experiments were made in primary and secondary forests near the villages of Baitabag (145°47' E, 5°08' S at ca. 50 m), Ohu (145°41' E, 5°14' S at ca. 100 m) and Riwo (145°48' E, 5°09' S at 0 m) as described by Basset *et al.* (1997).

(b) Host specificity

Ficus hispidooides was selected for experiments and observations on the basis of abundance in the study area and the baseline data of Godfray (1988). A pollination experiment in *F. hispidooides* (figure 1) was carried out during July and August 1997 in order to test for pollinator host specificity. Four treatments were included: (i) open pollination without any experimental manipulation, (ii) pollinator exclusion, (iii) intraspecific pollination by *Ceratosolen dentifer*, the obligate pollinator, and (iv) interspecific pollination by *Ceratosolen hooglandi*, the pollinator of the sympatric sister species *Ficus bernaysii* (Weiblen 2000). Pollinators were excluded from figs in treatments (ii)–(iv) by sealing the ostiole prior to receptivity with 1.5-ml screw-cap microcentrifuge tubes (Sarstedt¹). A hole was drilled in the cap of each tube and

attached to the fig with Liquid Nails¹ contact cement so that the ostiolar bracts were sealed by a removable container (figure 1). It was also necessary to replace the closed end of the tubes with 0.1 mm nylon mesh in order to allow the escape of fluid from the ostiole. On the day prior to pollination, pollinators were reared overnight in the laboratory from ripe gall figs. Live pollinators were transferred to tubes (6–25 pollinators each), cooled in an ice chest and assigned to specific treatments. Pollinators revived on reaching ambient temperature had either penetrated the ostiole or died in the tubes after 48 h. The number of founders per fig was estimated by subtracting the remaining wasps from initial counts.

(c) Pollination in gall and seed figs

The traits of gall and seed figs were compared with respect to wasp behaviour in order to examine the stability of pollination in *F. hispidooides* (figure 1a). The reproductive phenology of fig crops was monitored from June through to August in 1996 and 1997 at the Kau Wildlife Area and on the grounds of the Christensen Research Institute. Four gall and three seed trees were selected prior to inception (i.e. with bracts enclosing fig receptacles in bud). From 12 to 50 days after inception, the diameters of approximately five to ten figs per tree were measured to the nearest 0.1 mm at 48–96 h intervals. Data were pooled from the seven trees in order to obtain averages of fig diameter with respect to days from inception. The arrival of pollinators and non-pollinators at each tree was recorded through direct observation and through sticky traps fastened to the cauliflorous branchlets. Sticky traps consisted of Petri dishes (18.2 cm²) lined with Tanglefoot[®] and orientated vertically. A rolling census of the traps provided counts of fig wasp arrivals per 48–96 h.

Pollinator visitation rates and founder numbers in seed and gall figs were compared with Kruskal–Wallis tests. In addition, the diameters and weights of ripe figs, abundance of pistillate and staminate flowers per fig, seed set and percentage of ovules occupied by fig wasps were measured. A longitudinal section 2 mm in width from the base of the fig to the apex was removed and the flowers in one half section per fig were counted. Pistillate flowers were scored as containing either seeds, undeveloped ovules or galls as indicated by exit holes in the seed coat (Weiblen *et al.* 1995). Each count was multiplied by fig weight and divided by half the weight of the longitudinal section in order to obtain estimates for whole figs. Measurements of fig diameter, mass, ovule occupancy and style length from seed and gall figs were compared using nested analyses of variance with unequal sample sizes. The ratio of gall to seed plants in the study population was estimated and tested for parity using a *G*-test for goodness of fit.

(d) Host–parasitoid stability

The local fig wasp assemblage of sympatric *Ficus* species was sampled between 1995 and 1997 in order to examine the impact of non-pollinators on the mutualism. Rearing experiments with monoecious *Ficus microcarpa* and 14 functionally dioecious species (table 1) included a total of 207 crops (approximately ten figs per crop) collected from an average of ten trees per species. A key factor in stabilizing host–parasite interactions is parasitoid aggregation in space and time (May 1978; Hassell & Pacala 1990; Pacala *et al.* 1990). If the incidence of parasitism varies from fig to fig, then a high parasitoid density may reduce the efficiency of searching for pollinators (May 1978). A simple framework has been developed for testing whether heterogeneity

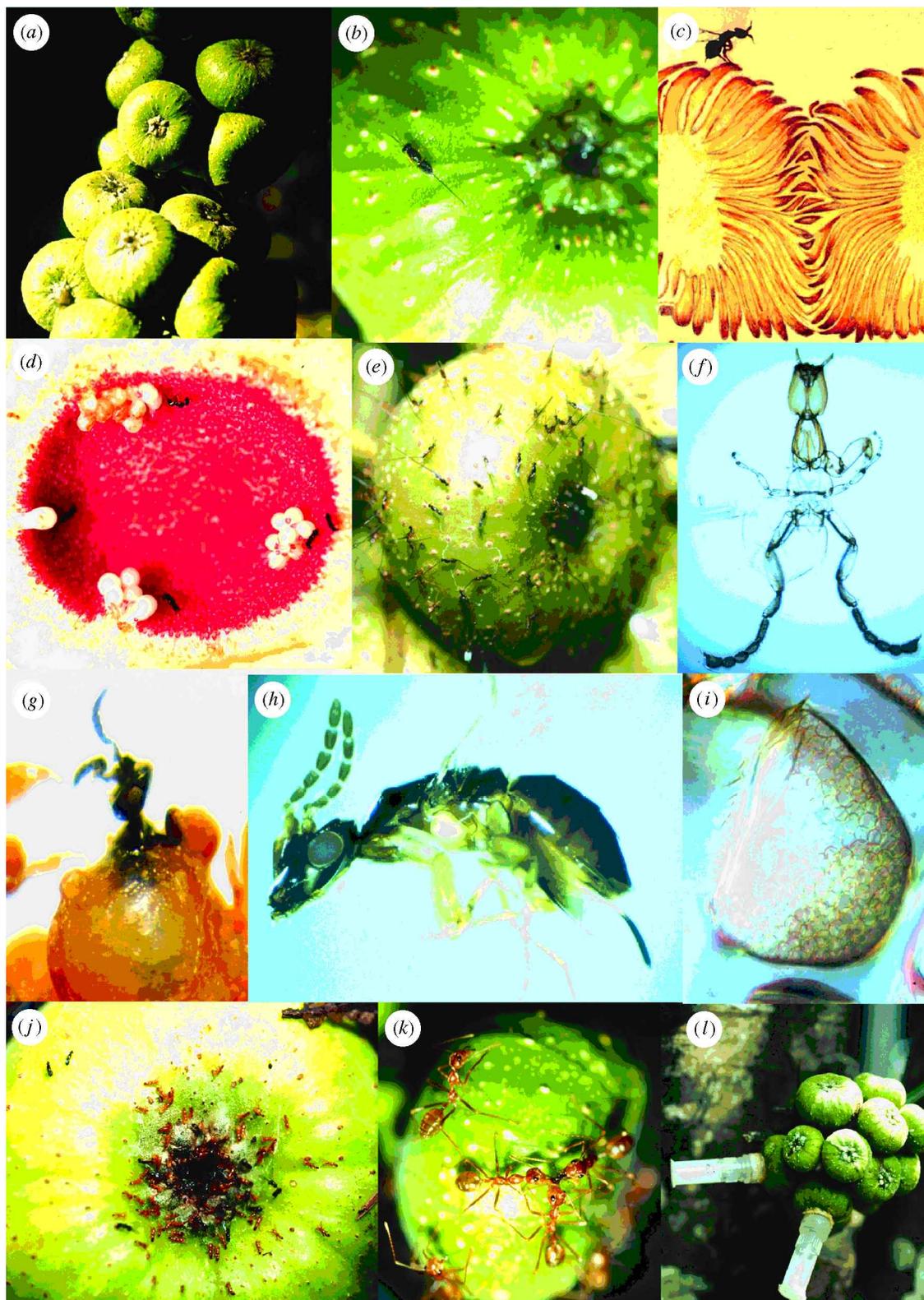


Figure 1. Illustrations of pollination and parasitism in functionally dioecious figs. (a) Cauliflorous *F. hispidioides* at Madang, Papua New Guinea. (b) Non-pollinating *Apocryptophagus* sp. (Sycophaginae) on a seed fig of *F. hispidioides*. (c) Drawing from Cunningham (1888) showing the arrival of *Ceratosolen* at the ostiole. (d) Five *C. dentifer* founders ovipositing in a gall fig of *F. hispidioides*; red pistillate flowers and white *Apocryptophagus* galls are also visible. (e) Parasitic *Philotrypesis* sp. ovipositing through the fig wall. (f) Male *C. hooglandi*, showing elongate hind tarsi. (g) Female *Ceratosolen appendiculatus* emerging from a gall in *F. variegata*. (h) Habitus of female *Ceratosolen armipes*. (i) Mesothoracic pocket in *Ceratosolen* sp. 'kaironkensis' containing *F. microdictya* pollen grains. (j) Male and female *C. dentifer* exiting through the ostiole of *F. hispidioides*. (k) Predatory ants (*Oecophylla smaragdina*) attacking *C. dentifer* on *F. hispidioides*. (l) Removable tubes excluding pollinators from the ostiole in *F. hispidioides*.

Table 1. *The incidence of pollinators, parasites and gallers in fig crops from monoecious Ficus microcarpa and 14 functionally dioecious species at Madang, Papua New Guinea*

| host spp. | wasp spp. per host | crops sampled | crops with pollinators (%) | crops with parasites (%) | crops with gallers (%) |
|-------------------------------|-----------------------|------------------|-------------------------------|-----------------------------|---------------------------|
| <i>Ficus microcarpa</i> | 14 | 9 | 56 | 67 | 100 |
| <i>Ficus bernaysii</i> | 5 | 15 | 100 | 80 | 80 |
| <i>Ficus botryocarpa</i> | 4 | 14 | 93 | 93 | 36 |
| <i>Ficus conocephalifolia</i> | 3 | 15 | 100 | 93 | 0 |
| <i>Ficus copiosa</i> | 3 | 19 | 100 | 47 | 53 |
| <i>Ficus dammaropsis</i> | 2 | 16 | 100 | 63 | 0 |
| <i>Ficus hispidooides</i> | 6 | 15 | 100 | 87 | 60 |
| <i>Ficus nodosa</i> | 6 | 17 | 100 | 65 | 88 |
| <i>Ficus phaeosyce</i> | 3 | 10 | 100 | 90 | 20 |
| <i>Ficus pungens</i> | 4 | 17 | 100 | 76 | 0 |
| <i>Ficus septica</i> | 5 | 14 | 100 | 93 | 14 |
| <i>Ficus tinctoria</i> | 6 | 8 | 100 | 100 | 25 |
| <i>Ficus trachypison</i> | 5 | 15 | 100 | 100 | 93 |
| <i>Ficus variegata</i> | 5 | 14 | 100 | 57 | 93 |
| <i>Ficus wassa</i> | 6 | 14 | 100 | 57 | 85 |

in the rate of parasitism has the potential to stabilize a host–parasitoid system. Heterogeneity can be divided into components that are dependent on host density and independent of host density, either of which can contribute to the stability of an interaction. *Ficus trachypison* was selected for examining heterogeneity in the rate of parasitism because this species had the simplest host–parasitoid system for examining the basic dynamics of the interaction. We performed a logistic regression of the relationship between pollinator (host) density and the rate of parasitism following Hails & Crawley (1992) in 15 crops from *F. trachypison* with an average of 19 figs per crop. The analysis of covariance was conducted using crop as a factor and pollinator density as a continuous variable.

3. RESULTS

(a) *Host specificity*

Attempts to introduce sympatric *C. hooglandi*, the pollinator of *F. bernaysii*, to figs of closely related *F. hispidooides* were unsuccessful. Seven out of 102 *C. dentifer* females entered figs of *F. hispidooides* whereas not one out of 75 *C. hooglandi* females visited *F. hispidooides* (Fisher's exact test, two-tailed $p = 0.021$).

(b) *Pollination in seed and gall figs*

The timing of wasp arrivals at figs was synchronized with reproductive phenology (figure 2a) and the period of development from inception to pollination lasted approximately two to three weeks. During the second week, female *Apocryptophagus* probed the fig exterior (figure 1b) and some pistillate flowers in both seed and gall figs were relatively enlarged by the third week (figure 1d). These observations, combined with the rearing of adults from both seed and gall figs, confirm that *Apocryptophagus* does not depend on pollinator larvae for inducing galls.

Female *C. dentifer* were trapped at figs between 14 and 28 days with peak visitation at 20–26 days (figure 2a). Females probed pistillate flowers inside the fig cavity with their ovipositors while transferring pollen from mesothoracic pockets to the stigmatic surface (figure 1d). Non-pollinating fig wasps were trapped 26–42 days following inception

(figure 2a). Female *Sycoscapter*, *Philotrypesis* and *Apocrypta* spp. (Sycoryctinae) probed the syconium exterior, each with a specially modified ovipositor (figure 1e). Although *Philotrypesis* and *Sycoscapter* were observed at both gall and seed figs, none were reared from seed figs. These observations suggest that *Philotrypesis* and *Sycoscapter* are parasitoids and depend on the presence of pollinator larvae to complete development. Relative body sizes further supported the conclusion of Godfray (1988) that *Apocrypta* is a hyperparasitoid of *Apocryptophagus*. Trophic interactions are summarized in figure 2b.

The ratio of gall and seed figs in *F. hispidooides* was not significantly different from parity and the rates of visitation indicated that pollinators do not distinguish between the two types (table 2). Non-pollinators were trapped in lower numbers than pollinators and there was also no significant difference in the rate of non-pollinator visitation to gall and seed figs. In addition, the average numbers of founders in gall and seed figs were substantially higher than in neotropical monoecious figs (Herre 1989). Herre (1989) showed that founder numbers affect male and female function differently but we found no evidence for different founder numbers in gall figs and seed figs (table 2). It was not possible to control for the effect of founder number on seed set and pollinator production owing to the deterioration of *C. dentifer* in fluid-filled figs. Ripe gall figs were significantly larger in diameter than seed figs although the difference in fresh weight was not significant. Similar to other functionally dioecious species, style length in *F. hispidooides* was bimodally distributed between gall figs and seed figs (figure 2c) with styles in seed figs exceeding the length of *C. dentifer* ovipositors.

(c) *Host–parasitoid stability*

A species accumulation curve for the fig wasp assemblage of 15 sympatric *Ficus* species is shown in figure 2d. Seventy-eight morphospecies were reared from 207 crops and exhaustive sampling may have yielded six additional species according to Chao's non-parametric method based on species incidence (Colwell & Coddington 1994) and

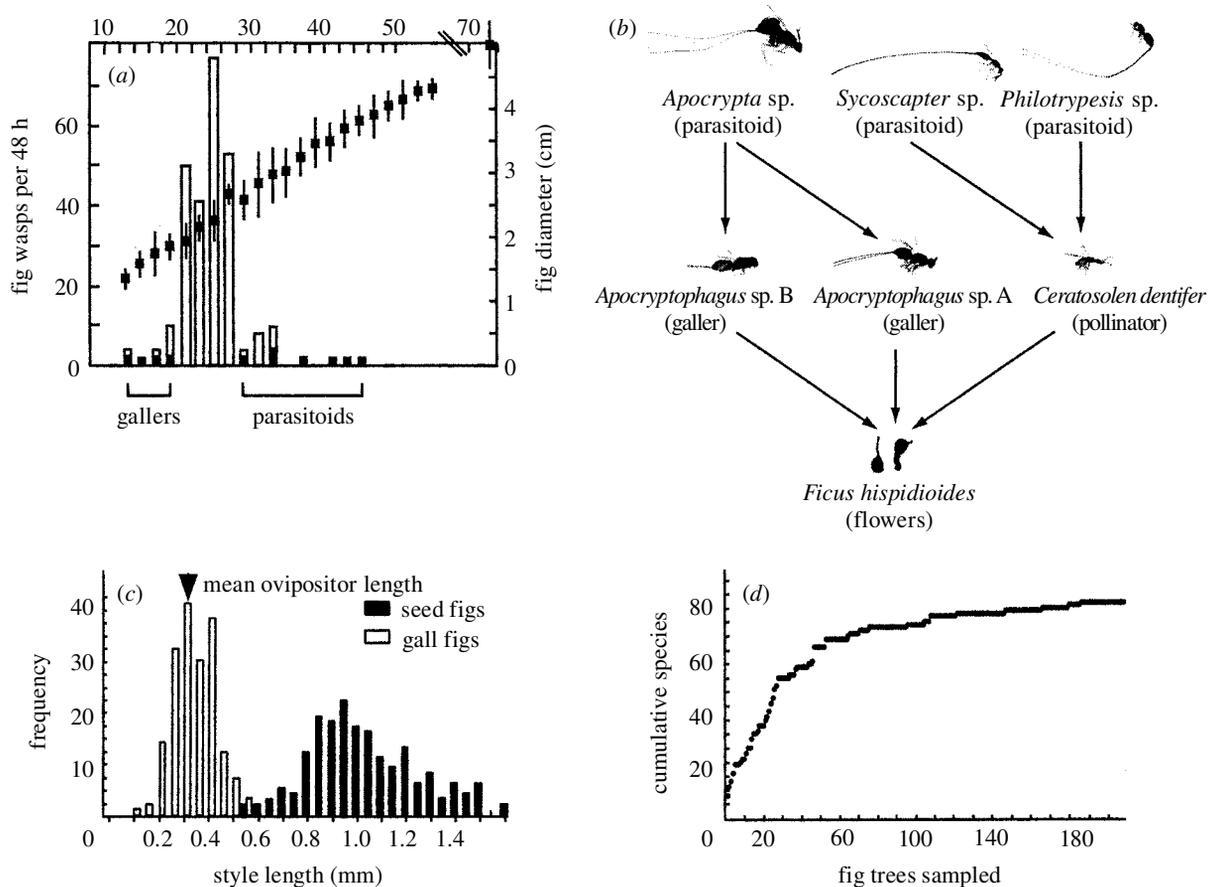


Figure 2. (a) Timing of fig wasp arrivals at *F. hispidooides* at Madang, Papua New Guinea. The numbers of pollinators (open bars) and non-pollinators (closed bars) trapped at figs during 48 h intervals and the mean fig diameter (error bars indicate standard deviations) are plotted against fig age (days after inception). Gallers and parasitoids (indicated in brackets) arrived prior to and after the peak in pollinator visitation, respectively. (b) Trophic interactions in figs of *F. hispidooides*. Arrows indicate the feeding relationships between pollinators, gallers and parasitoids. The illustrations are scaled to show relative differences in ovipositor length and body size among the different guilds. (c) Style length dimorphism in *F. hispidooides*. Gall figs (open bars) contained only short-styled pistillate flowers (0.1–0.5 mm) while seed figs (closed bars) contained only long-styled flowers (0.6–1.6 mm). There was no difference between fig crops of the same sex. (d) Species accumulation curve for the fig wasp assemblage of 15 sympatric *Ficus* species at Madang, Papua New Guinea. A total of 78 putative fig wasp species were reared from 214 fig crops collected from separate trees. The sampling order of trees was randomized following Colwell & Coddington (1994).

similar totals may be obtained using the program EstimateS (v. 5, R. K. Colwell, unpublished data). Unique pollinator species were consistently associated with each fig species and a large assemblage of undescribed non-pollinating Agaonidae was also found. On average, there were between three and four non-pollinating species per host, ranging from one in *Ficus dammaropsis* to 13 in *F. microcarpa*.

There were at least two feeding modes among non-pollinators: gallers competing with pollinator larvae for fig ovules and parasitoids killing pollinator larvae and feeding on fig endosperm (Godfray 1988). *Sycosapter* and *Philotrypesis* (Sycoryctinae) oviposited after the pollinators and are probably parasitoids (Kuttamathiathu 1959). *Apocryptophagus* (Sycophaginae) galled both types of figs, and the larvae appeared to feed on proliferating nucellus as in other Sycophaginae (Galil *et al.* 1980). Parasitic *Apocrypta* (Sycoryctinae) were reared from seed and gall figs in which *Apocryptophagus* were present. *Grandiana* (Otitesellinae), *Epichrysomalla* and *Neosycophila* (Epichrysomallinae) are also thought

to be gallers (Boucek 1988), but they were not reared from seed figs.

All the functionally dioecious species had a lower incidence of parasitism than the single monoecious species censused. In functionally dioecious species, pollinators occurred in 93–100% of the crops, while in monoecious *F. microcarpa* pollinators were present in only 56% (table 1). There were also more non-pollinator species associated with *F. microcarpa* (13) than with any functionally dioecious host (one to five). The abundance of non-pollinators within figs also differed between monoecious and functionally dioecious species. *Ficus microcarpa* had a similar abundance of pollinators and non-pollinators (3.4 pollinators per fig versus 5.4 *Odontofrogatia* gallers on average). In contrast, the average pollinator abundance in functionally dioecious species was consistently several times greater than the combined abundance of non-pollinators.

The distribution of pollinator abundance per fig was not significantly different from normal when pooled across 15 crops from *F. trachypison* (figure 3a) ($\chi^2 = 24.7$,

Table 2. *Comparisons of gall and seed fig traits in Ficus hispidooides*

(The frequency of gall and seed trees at the Kau Wildlife Area, Madang, Papua New Guinea, was compared against an even sex ratio with a *G*-test for goodness of fit. Mean pollinator visits and founders per fig in gall and seed figs were compared with Kruskal–Wallis tests. Nested analyses of variance compared fig diameter, fig mass, ovule occupancy and style length between gall and seed figs. Diameter (cm) and mass (g) are reported for ripe figs.)

| | gall figs | | seed figs | | test | |
|----------------------------|-----------------|----------|-----------------|----------|-----------|-----------------|
| | <i>X</i> (s.e.) | <i>n</i> | <i>X</i> (s.e.) | <i>n</i> | statistic | <i>p</i> -value |
| census (number of trees) | 18 | — | 21 | — | 0.231 | n.s. |
| pollinators per trap | 22.6 (5.8) | 3 | 22.0 (4.7) | 8 | 0.041 | n.s. |
| non-pollinators per trap | 0.9 (0.6) | 3 | 1.7 (0.3) | 8 | 0.503 | n.s. |
| founders per fig | 5.0 (1.8) | 6 | 5.7 (1.4) | 3 | 0.610 | n.s. |
| fig diameter (cm) | 5.1 (0.1) | 41 | 4.7 (0.1) | 38 | 20.48 | < 0.001 |
| fig mass (g) | 51.9 (2.5) | 41 | 46.4 (1.8) | 38 | 3.092 | n.s. |
| pistillate flowers per fig | 3749 (312) | 20 | 4125 (625) | 11 | 3.719 | n.s. |
| staminate flowers per fig | 100 (10) | 20 | 0 (—) | 11 | — | — |
| percentage seed set | 0 (—) | 20 | 85.6 (3.2) | 11 | — | — |
| percentage wasp occupancy | 52.3 (4.3) | 20 | 0 (—) | 11 | — | — |
| style length (mm) | 0.35 (0.01) | 170 | 1.05 (0.02) | 190 | 1539 | < 0.0001 |

d.f. = 15 and n.s.), whereas the galler and parasitoid abundances were highly different from a normal distribution ($p < 0.0001$) due to the large proportion of figs that lacked non-pollinators (figure 3*b,c*). This result suggests strong limits on the rates of arrival or oviposition in non-pollinators. At the fig level, a logistic regression indicated that pollinator abundance was negatively correlated with galler abundance (F -ratio = 35.33, d.f. = 1 and $p < 0.0001$) suggesting competition between mutualists and parasites. In addition, there was a significant negative relationship between pollinator density and the rate of parasitism (inverse density dependence) (figure 3*d*) (Hassell *et al.* 1985) as revealed by logistic regression ($F = 46.32$, d.f. = 1 and $p < 0.0001$), as well as significant variation between crops in the rate of parasitism ($F = 3.55$, d.f. = 15 and $p < 0.0001$). However, the crop effect was only marginally significant ($F = 1.62$, d.f. = 14 and $p = 0.075$) when a single crop with low pollinator density was excluded from the analysis. The crop effect and pollinator density together accounted for only 31.9% of the total variance in the rate of parasitism, indicating that both host density independence and host density dependence contribute to host–parasitoid stability with the former being more important, as has been found in other host–parasitoid systems (Pacala *et al.* 1990). The results were similar if gallers were added to the analysis as potential hosts, but the total variance explained by crop and host density was lower (20.2%).

4. DISCUSSION

(a) *Host specificity*

Artificial pollination in *F. hispidooides* was consistent with inferences of host plant specificity based on rearing experiments. Pollinators appeared to be monophagous and were not forced to switch between closely related fig species, although larger sample sizes are needed to support this tentative conclusion. The behaviour of *C. dentifer* was similar to other species of *Ceratosolen* (Baker 1913; Galil & Eisikowich 1968*b*; Galil 1973; Joseph &

Abdurahiman 1981; Kerdelhue *et al.* 1997) that are able to distinguish a particular host species from its close relatives in sympatry using olfactory cues released by receptive figs (Hossaert-McKey *et al.* 1994). The assumption of one-to-one host specificity has been applied to non-pollinators (Ulenberg 1985; Machado *et al.* 1996), but further taxonomic revisions and phylogenetic analyses are needed in order to make a stronger assessment of host range in these taxa.

(b) *Stability of functional dioecy in Ficus*

As in other functionally dioecious species (Nair & Abdurahiman 1984; Beck & Lord 1988; Corlett *et al.* 1990; Weiblen *et al.* 1995), resource conflicts were apparent between *F. hispidooides* and *C. dentifer* (Kjellberg *et al.* 1987; Grafen & Godfray 1991). In particular, pollinators showed no avoidance of seed figs despite total failure to reproduce in them. The simplest explanation for seed fig pollination is deception. Stabilizing selection would favour seed figs that mimic gall figs in attractiveness and prevent pollinators from discriminating against them (Grafen & Godfray 1991). Patel *et al.* (1995) pointed out the difficulty in detecting less stable interactions because the evolution of gall fig preference in pollinators would rapidly drive host plants to extinction. However, functionally dioecious fig lineages are no less diverse than monoecious lineages (Weiblen 2000), suggesting that functional dioecy is no more extinction prone than monoecy.

Functionally dioecious figs also pose an interesting problem related to pollination and seed dispersal (Laman & Weiblen 1998). The similar external appearance of both types of fig prior to pollination may limit pollinator avoidance of seed figs, but after pollination it is advantageous for seed figs to be dispersed by frugivores and for gall figs to remain on the plant. Although gall and seed figs appear similar prior to pollination, they ultimately differ in size, coloration and palatability when ripe (table 2) (Lambert 1992; Weiblen *et al.* 1995). Indeed, ripe gall figs are often ignored by frugivores that prefer to eat seed figs of the same species, even though gall figs tend to

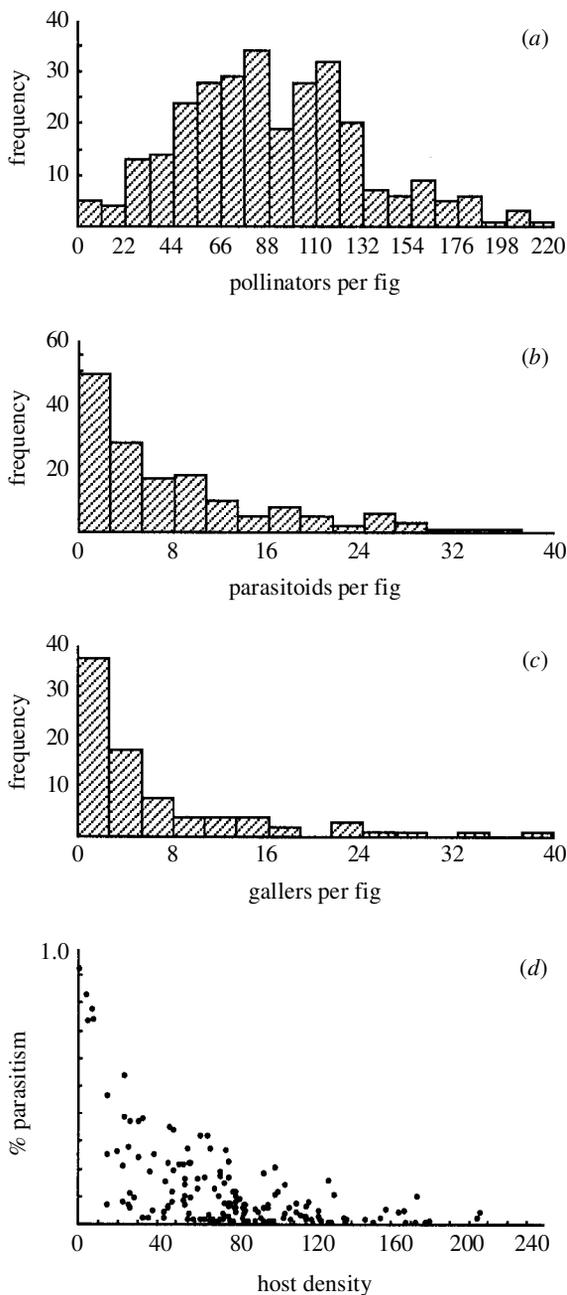


Figure 3. Abundances of (a) pollinators, (b) parasitoids and (c) galls per fig in *F. trachypison* at Madang, Papua New Guinea. The numbers of pollinators per fig were distributed normally in 288 samples from 15 different crops. The distribution of non-pollinators per fig deviated significantly from a Poisson distribution due to the absence of parasites and galls from 134 and 204 out of 288 figs, respectively. (d) The inverse density-dependent relationship between pollinator abundance and the frequency of parasitism in *F. trachypison*.

be larger (Laman & Weiblen 1998). Gall and seed fig similarity during the pollination phase could be opposed by selection favouring dissimilarity during the dispersal phase. Disruptive selection in functionally dioecious figs is an intriguing possibility for future study.

(c) Stability of parasitism in functionally dioecious figs

To the authors' knowledge, this is the first study to compare rates of parasitism in monoecious and functionally

dioecious species from the same locality. Non-pollinators had a direct negative impact on pollinators and an indirect impact on functionally dioecious figs. Gallers competed with pollinators for seed resources and parasitoids attacked pollinator larvae. All gallers of functionally dioecious figs apart from *Apocryptophagus* were restricted to gall figs and it is unclear why most gallers are limited to the same flowers as the pollinators (West *et al.* 1996). The incidence of parasitism in New Guinea figs was also consistent with a general trend towards fewer non-pollinator species in functionally dioecious figs than in monoecious *F. microcarpa* (table 1) (Kerdelhue & Rasplus 1996). However, these observations do not address the question of what enables the coexistence of gallers and pollinators in functionally dioecious figs.

Following May (1978), in order to achieve dynamic coexistence the heterogeneity of predation risk must be greater than that produced by chance alone, that is more heterogeneous than a Poisson distribution. At least three sources of heterogeneity could contribute to stabilizing the interaction, including host density dependence, host density independence and between-crop variation. For example, West *et al.* (1996) reported that positive host density-dependent heterogeneity was sufficient for stabilizing the interaction between parasitic *Physothorax* and *Aepocercus* in a monoecious fig. The host density-independent aggregation of parasitoids appears to be the most important factor in *F. trachypison*. In contrast to West *et al.* (1996), we observed an inverse relationship between the rate of parasitism and pollinator density in *F. trachypison* (figure 3d). Hassell *et al.* (1985) attributed inverse density dependence to a low upper limit on the rate of parasitism per patch and little or no aggregation of parasitoids within patches. Rearing data suggested that both of these processes may be operating at the crop level in *F. trachypison*. The frequency of parasitism per fig never exceeded 10% on average and there was no significant variation in the frequency of parasitism among ten crops. What factors could limit the rate of parasitism within patches and explain the non-aggregation of parasites at the crop level? Possibilities include the rarity of receptive trees at any point in time, a failure of parasitoids to detect figs with high pollinator density or a failure to determine where parasitoid eggs have been laid. In particular, ant predation was observed while *Philotrypes* probed for oviposition sites (figure 1e–k) and this could impose a limit on parasitoid search time (Cushman *et al.* 1998). In addition, we argue below that the efficiency of parasitoid searching may also be reduced by the presence of seed figs.

(d) Advantages of functional dioecy in Ficus

Our observations also bear on hypotheses for the evolution of functionally dioecious fig pollination. Kerdelhue & Rasplus (1996) proposed that a reduction of ovary layers in gall figs compared with monoecious figs could limit the incidence of non-pollinators. Alternatively, search time wasted on seed figs could account for the lower species richness of non-pollinators in functionally dioecious *Ficus*. The trap data from *F. hispidooides* (table 2) support this idea because non-pollinators appeared not to avoid seed figs in the search for oviposition sites. Seed figs could serve as ecological sinks in which time wasted by

Table 3. *Abundance and frequency of pollinators, parasitoids and galls per fig in Ficus trachypison at Madang, Papua New Guinea*

| | X (s.e.) | n | minimum | maximum |
|----------------------------------|-------------|-----|---------|---------|
| pollinators per fig | 89.3 (2.5) | 288 | 1 | 209 |
| parasitoids per fig | 8.2 (0.6) | 154 | 1 | 36 |
| galls per fig | 6.4 (0.9) | 84 | 1 | 40 |
| total wasps per fig | 95.6 (2.3) | 288 | 20 | 215 |
| frequency of parasitoids per fig | 0.12 (0.01) | 154 | 0.005 | 0.92 |
| frequency of galls per fig | 0.09 (0.01) | 84 | 0.008 | 0.46 |
| frequency of non-pollinators | 0.09 (0.01) | 288 | 0 | 0.96 |

parasitoids could reduce levels of parasitism in gall figs, leading to increased pollinator production.

The parasitoid–sink hypothesis is illustrated through a simple model of pollinator production. Suppose that, in a fig population, X equals the number of pollinator-producing trees, Y equals the number of pollinators produced per tree and Z equals pollinator survivorship. Pollinator production in a monoecious population is then defined as

$$P_M = (X)(Y)(Z). \quad (1)$$

In a functionally dioecious population, pollinator production would be

$$P_D = (X/2)(2Y)(aZ),$$

where gall figs are half the population ($X/2$), but where pollinator production is doubled ($2Y$) in these figs relative to monoecious figs due to the presence of twice as many accessible ovules. Reduced parasitism in gall figs also increases pollinator survivorship relative to monoecious figs by a factor of a . As a result, pollinator production in a functionally dioecious population will exceed that of a monoecious population ($P_D > P_M$) by a . An increase in pollinator production due to functional dioecy could be particularly advantageous in seasonal climates where pollinators are limiting (Kjellberg & Maurice 1989; Spencer *et al.* 1996).

The assumption of an equal sex ratio in functionally dioecious figs is supported by population census data from *F. hispidioides* (table 2) and *Ficus variegata* (G. Weiblen, unpublished data) and by progeny arrays from *Ficus carica* (Storey 1955). The assumption of increased pollinator production in gall figs relative to monoecious figs is also supported by census data (Corlett 1993; Weiblen *et al.* 1995; Kerdelhue *et al.* 1997). The doubling of pollinator production in gall figs relative to monoecious figs could be due to more efficient oviposition in short-styled flowers (Nefdt & Compton 1996). The magnitude of the increase in pollinator survivorship in gall figs depends on how much time parasitoids spend on seed figs and more empirical data are needed in order to address this point. If parasitoids spend equal time searching gall and seed figs, then a equals two and a functionally dioecious population would produce twice as many pollinators as a monoecious population with no corresponding decrease in seed production. In contrast, lower search efficiencies for non-pollinators should reduce population growth rates and sizes, leading to higher rates of extinction and lower rates of invasion.

Thus, a reduction in parasitism through functional dioecy is advantageous for both the pollinator and the host plant, particularly in environments where pollinators are limiting as in seasonal climates (Bronstein 1989). Parasitism might therefore have played a role in the origin, maintenance and geographical spread of dioecious fig pollination. Sister-group comparison of monoecious and functionally dioecious species under similar ecological conditions would aid in testing this idea with more data on seed set, pollinator production and rates of parasitism.

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