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A mutualism at the edge of its range

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Summary. Comparing populations that differ in access to mutualists can suggest how traits associated with these interactions have evolved. I discuss geographical and seasonal variation in the success of a primarily tropical mutualism (the fig/pollinator interaction), and evaluate some possible adaptations allowing it to persist at the edge of its range. Pollinators probably have difficulty in seasonal sites because 1) fig trees flower rarely in winter and 2) trees that do flower are less detectable and more difficult to reach. Fig biologists believe that seasonality must have selected for adaptations allowing pollinators to survive winter. However, geographical comparisons do not support two current ideas, the synchrony-breakdown hypothesis and the specificity-breakdown hypothesis. I pose two alternatives: plasticity of fruit and wasp developmental time, and adaptations of free-living fig wasps. I also distinguish between the impact of seasonality on monoecious versus dioecious figs; the latter group appear better adapted to reproduce in cool climates. A combination of comparative, observational, and experimental approaches has great potential for advancing our understanding of mutualisms.

Key words. Agaonidae; coevolution; *Ficus*; fig; mutualism; phenology; pollination; seasonality.

Introduction

Coevolved mutualisms can only persist in places that both partners can reach, and can survive and reproduce in once there. This simple constraint has profound consequences for the ecology and evolution of species dependent upon mutualists. Mutualisms (particularly obligate ones) commonly involve organisms of distant taxa[14], and their ecological requirements must often be widely divergent. A species whose mutualist is excluded from a given location may be unable to invade[35,71], may interact with an alternative partner[10,34], or may stop relying upon mutualists altogether[73,101], either on an ecological or evolutionary time scale. However, even if both partners are present, environmental conditions are likely to

be more harsh for one of them. The success of the mutualism itself will therefore vary in space, as will selection pressures on it. Environment-specific selection pressures lead to the possibility of environment-specific adaptations over the range of a single mutualistic interaction. Few data are available on geographic variation within mutualisms, because these interactions have nearly always been studied at a single site[7,39,66,84,99]. Even basic information about the components of a particular mutualistic interaction that are most sensitive to environmental variation is rare. My intention here is to review information on geographic and seasonal variation in the success of a primarily tropical mutualism, the fig/pollina-

tor interaction, and to critically examine some suggested adaptations allowing it to persist at the edge of its range. The obligate interaction between figs (*Ficus* spp., Moraceae) and their pollinators (Hymenoptera: Agaonidae) is exceptionally common and widespread. There are probably over 700 species pairs worldwide[9]. Figs and their pollinators evolved and are most abundant in the equatorial tropics, but representatives are present as distant as 45° north and 35° south latitude. (Detailed distributions are given by Berg[9]). This mutualism offers three distinct advantages for studying patterns of geographical variation. First, the consequences of poor survival or reproduction of each mutualist are strong and straightforward: if fig trees of a given species fail to flower, their pollinators will rapidly die off, and if pollinators cannot survive the flight between trees, the trees will not set fruit. Second, it is easy to identify one aspect of environmental variation, namely seasonality, that should affect the success of both partners, and thus of their interaction. During cool periods, fig wasp survival and flight ability are strongly limited, and fig trees initiate flowering much more rarely. Lastly, a small but growing data base is available for studying patterns of variation in fig traits. Ecological studies have been carried out on about 50 species over a broad geographical range (fig. 1). In a few cases, the same fig-pollinator pair has been studied in different parts of its range; because the interaction itself is fairly stereotyped, comparisons can also be drawn (with caution) among groups of species pairs in contrasting regions.

I first examine the factors that should determine whether fig wasps will successfully locate a tree, and consider which of these should be affected by climatic variation. Identifying such 'weak points' in the interaction suggests where selection may have acted in the past for the mutualism to now persist in some seasonal habitats. With this goal in mind, I then describe some unusual attributes of fig species that have been studied in strongly seasonal sites, and relate them to two current hypotheses explaining how the mutualism can function under such conditions. I also consider alternatives to those hypotheses. While I will concentrate on the much more throughly studied monoecious fig species (half of the genus), the last section contrasts these with the dioecious species, a group perhaps better adapted to persist in seasonal environments.

Factors regulating pollination/oviposition success

A model of interacting fig and pollinator populations

The interaction between monoecious figs and their pollinators that is now considered 'typical' is based on the classic studies of *Ficus sycomorus* by J. Galil and D. Eisikowitch in East Africa[47, 50, 51, 52]. It can be summarized briefly as follows[17, 18, 46, 65, 74, 94, 116] (table 1). Pollen-carrying female wasps arrive at a tree bearing several hundred or thousand inflorescences, or syconia.

Each one is a hollow structure (a multiple receptacle) lined with hundreds of florets. At the time the wasps arrive, only the female florets are receptive. The wasps enter the syconia via the ostiole, becoming trapped in the process. Once inside they deposit pollen on the stigmas, then oviposit directly into some of the ovaries. A mixture of seeds and seed-eating wasp larvae develops over the next several weeks. When the wasps are mature, they copulate. Females then collect pollen from the newly mature anthers, while males tunnel back through the wall of the fig. The female wasps then depart, in search of syconia in which to oviposit. As a rule, syconia on an individual tree are highly synchronized, whereas different trees flower out of synchrony. Therefore, the wasps must locate another tree in the correct sexual phase. They have little time in which to do so; free-living adults do not feed and survive several days at most.

The rapid location of flowering trees by the fig wasps is clearly in the selective interests of both partners. What factors determine whether a successful match will occur? To address this question, it is necessary to examine the availability of flowering trees and searching wasps at the population level.

First, consider that there are three possible outcomes of a given reproductive cycle for a monoecious fig tree (fig. 2a). A tree can successfully attract pollinators during its brief female phase, and several weeks later the departing offspring of those wasps can successfully deliver pollen to another tree. That tree is therefore fertile in both its male and female phases. Alternatively, the tree can successfully attract pollinators, but when the pollen-loaded offspring of those wasps depart several weeks later, there may not be another tree flowering close enough in time or space for them to reach. That tree is therefore fertile in its female phase but sterile as a male or pollen-donor. Finally, the tree might flower at a time or place where no searching pollinators are present; it will be sterile both as a female and as a male.

The frequency of these three outcomes depends on the flowering pattern at the level of the fig population. Flowering within a hypothetical three-tree population is illustrated in figure 3a. Two points are critical. First, population-level flowering asynchrony is clearly essential for

Table 1. Developmental phase of monoecious figs as defined by Galil and Eisikowitch.

| Phase	Description
Phase A (pre-female):	young syconium prior to the opening of the ostiole.
Phase B (female):	ostiolar scales loosen, female flowers ripen, pollinators penetrate into the syconium and oviposit into the ovaries.
Phase C (interfloral):	wasp larvae and fig embryos develop within their respective ovaries.
Phase D (male):	male flowers mature, wasps reach the imago stage, fertilized female wasps leave the syconia via tunnels bored by the males.
Phase E (post-floral):	both the syconia and the seeds inside them ripen.
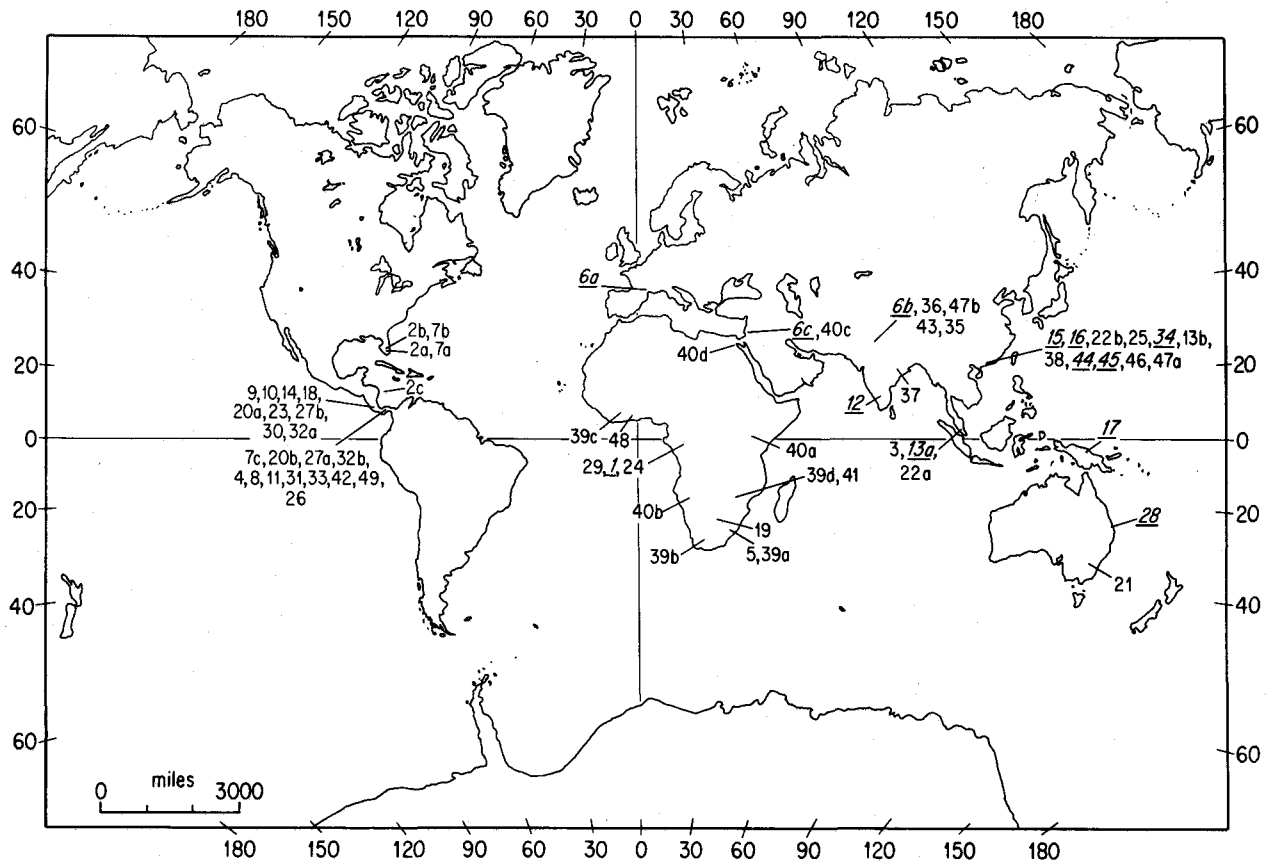
Figure 1. Geographical distribution of fig species for which there is published information (through 1988) on their interaction with pollinators in their native habitats. Each number refers to one species. In cases where the species has been studied in different locations, each location is as-

signed a different letter. Italicized numbers are dioecious species; all others are monoecious. The Appendix lists species names, data on study sites, and references.

wasps to move successfully between trees, and thus for trees and wasps both to reproduce. Moreover, such asynchrony must extend *year-round*; if trees cannot initiate flowering for a period of time, the local wasp population will go extinct, and no tree will reproduce again until wasps recolonize. The proximate causes of this population-level asynchrony are the somewhat variable durations of reproductive episodes, and the extremely variable intervals between reproductive episodes.

The second critical point is that reproductive failure should be very common even when flowering is asynchronous enough for pollinators to persist year-round. Of the seven complete reproductive cycles shown in figure 3a, two fail entirely because the female phase fell at a time when no searching pollinators were available. One other cycle is successful only in the female phase, because the pollen-carriers departing from it could reach no flowering neighbour. Furthermore, success is relative: for example, in the simple case presented here, pollen-carriers can arrive from either one or two neighbors.

The general validity of this simple phenological model can be tested by asking whether reproductive success is in fact highly variable within monoecious fig populations. Quantitative data are available for few species, and

only for the female component of reproductive success[15-17, 65, 85, 87]. These data do, however, support the prediction. For example, Bronstein[17] found that the proportion of syconia entered by pollinators (and consequently, the proportion matured) ranged from one to 100% among 21 *F. pertusa* crops studied over two years in Costa Rica, and averaged only 65%. Two crops attracted almost no pollinators. Furthermore, differences among crops in the number of pollinators per entered syconium were highly significant[15]. The number of arriving pollinators caught on sticky traps placed in some trees reflected this great variation[17].

Factors determining the number of searching wasps
Inspection of this phenological model suggests a number of factors that will determine whether a successful 'match' between figs and pollinators will occur. First, fig trees should on average attract more pollinators if there are more pollinators that begin to search for them. That number should increase with both the number of trees from which wasps are departing, and the number of wasps departing per tree. Here, I consider only the former limiting factor because so little is yet known about limits to fig wasp production within trees. It seems to be

Appendix. Key to the *Ficus* species mapped in figure 1. Underlined species numbers are dioecious; all others are monoecious.

Number in Figure	Species	Site	Latitude	Longitude	Reference
1	*asperifolia*	Makokou, Gabon	0°04′ N	12°52′ E	114
2a	*aurea*	Everglades, USA	26°40′ N	80°38′ W	41, 42
2b		Coral Gables, USA	25°43′ N	80°16′ W	this study
2c		San Andres, Colombia	12°32′ N	81°42′ W	94
3	*benjamina*	Singapore	1°17′ N	103°50′ E	30
4	*bullenei*	Barro Colorado, Panama	9°09′ N	79°51′ W	65
5	*burtt-davyi*	Durban, S. Africa	29°50′ S	31°00′ E	3
6a	*carica*	Montpellier, France	43°36′ N	3°53′ E	79, 81, 109, 110, 111
6b		Delhi, India	28°40′ N	78°13′ E	26
6c		Safad, Israel	32°57′ N	35°27′ E	54
7a	*citrifolia*	Everglades, USA	26°40′ N	80°38′ W	41, 42
7b		Coral Gables, USA	25°43′ N	80°16′ W	this study
7c		Barro Colorado, Panama	9°09′ N	79°51′ W	65
8	*colubrinii*	Barro Colorado, Panama	9°09′ N	79°51′ W	65
9	*costaricana*	San Jose, Costa Rica	9°56′ N	84°05′ W	56
10	*cotinifolia*	Santa Rosa, Costa Rica	11°03′ N	85°35′ W	75, 76
11	*dugandii*	Barro Colorado, Panama	9°09′ N	79°51′ W	65
12	*exasperata*	Calicut, India	11°15′ N	75°46′ E	5
13a	*fistulosa*	Singapore	1°17′ N	103°50′ E	31, 45
13b		Hong Kong	22°11′ N	114°10′ E	68
14	*hemsleyana*	San Jose, Costa Rica	9°56′ N	84°05′ W	56
15	*hirta*	Hong Kong	22°11′ N	114°10′ E	68
16	*hispida*	Hong Kong	22°11′ N	114°10′ E	68
17	*hispidioides*	Madang, Papua New Guinea	5°14′ S	145°45′ E	59
18	*hondurensis*	Santa Rosa, Costa Rica	11°03′ N	85°35′ W	75
19	*ingens*	Johannesburg, S. Africa	26°12′ S	28°05′ E	6
20a	*insipida*	Santa Rosa, Costa Rica	11°03′ N	85°35′ W	76
20b		Barro Colorado, Panama	9°09′ N	79°51′ W	65
21	*macrophylla*	Sydney, Australia	33°55′ S	151°10′ E	92
22a	*microcarpa*	Singapore	1°17′ N	103°50′ E	30
22b		Hong Kong	22°15′ N	114°10′ E	68
23	*morazaniana*	Santa Rosa, Costa Rica	11°03′ N	85°35′ W	76
24	*natalensis*	Makokou, Gabon	0°04′ N	12°52′ E	85
25	*nervosa*	Hong Kong	22°15′ N	103°50′ E	68
26	*nymphifolia*	Barro Colorado, Panama	9°09′ N	79°51′ W	65
27a	*obtusifolia*	Barro Colorado, Panama	9°09′ N	79°51′ W	65
27b		Santa Rosa, Costa Rica	11°03′ N	85°35′ W	75
28	*opposita*	Heron Island, Australia	23°25′ S	151°55′ E	63
29	*ottonifolia*	Makokou, Gabon	0°04′ N	12°52′ E	85, 87, 113
30	*ovalis*	Santa Rosa, Costa Rica	11°03′ N	85°35′ W	75, 76
31	*perforata*	Barro Colorado, Panama	9°09′ N	79°51′ W	65
32a	*pertusa*	Monteverde, Costa Rica	10°12′ N	84°12′ W	15, 16, 17, 18, 19, 20
32b		Barro Colorado, Panama	9°09′ N	79°51′ W	65
33	*popenoei*	Barro Colorado, Panama	9°09′ N	79°51′ W	65
34	*pyriformis*	Hong Kong	22°15′ N	103°50′ E	68
35	*racemosa*	Delhi, India	28°40′ N	78°13′ E	26
36	*religiosa*	Delhi, India	28°40′ N	78°13′ E	77
37	*roxburghii*	Calcutta, India	22°32′ N	88°22′ E	36
38	*superba*	Hong Kong	22°15′ N	103°50′ E	68
39a	*sur*	Durban, S. Africa	29°50′ S	31°00′ E	2
39b		Grahamstown, S. Africa	33°22′ S	26°29′ E	27
39c		Ivory Coast	–	–	115
39d		Harare, Zimbabwe	17°43′ S	31°05′ E	37
40a	*sycomorus*	Magadi, Kenya	4°03′ S	39°40′ E	47, 50, 53, 55
40b		Gobabeb, Namibia	23°34′ S	15°03′ E	118
40c		Tel Aviv, Israel	32°05′ N	34°48′ E	48
40d		Cairo, Egypt	30°03′ N	32°15′ E	22
41	*thonningii*	Harare, Zimbabwe	17°43′ S	31°05′ E	12
42	*trigonata*	Barro Colorado, Panama	9°09′ N	79°51′ W	65
43	*tsiela*	Delhi, India	28°40′ N	78°13′ E	26
44	*variegata*	Hong Kong	22°15′ N	103°50′ E	68
45	*variolosa*	Hong Kong	22°15′ N	103°50′ E	68
46	*vasculosa*	Hong Kong	22°15′ N	103°50′ E	68
47a	*virens*	Hong Kong	22°15′ N	103°50′ E	68
47b		Delhi, India	28°40′ N	78°13′ E	
48	*vogelii*	Kumasi, Ghana	6°42′ N	1°37′ W	26
49	*yoponensis*	Barro Colorado, Panama	9°09′ N	79°51′ W	88

A. MONOECIOUS

Male-fertile +
female-fertile

Female-fertile

Sterile

B. DIOECIOUS

Females:

Female-fertile

Sterile

Males:

Male-fertile

Sterile

Sterile

Sterile

Female-phase; flowers receptive

Male-phase; wasps leave

Fruit development

Syconium abscission

Wasp transfer

Wasp mortality
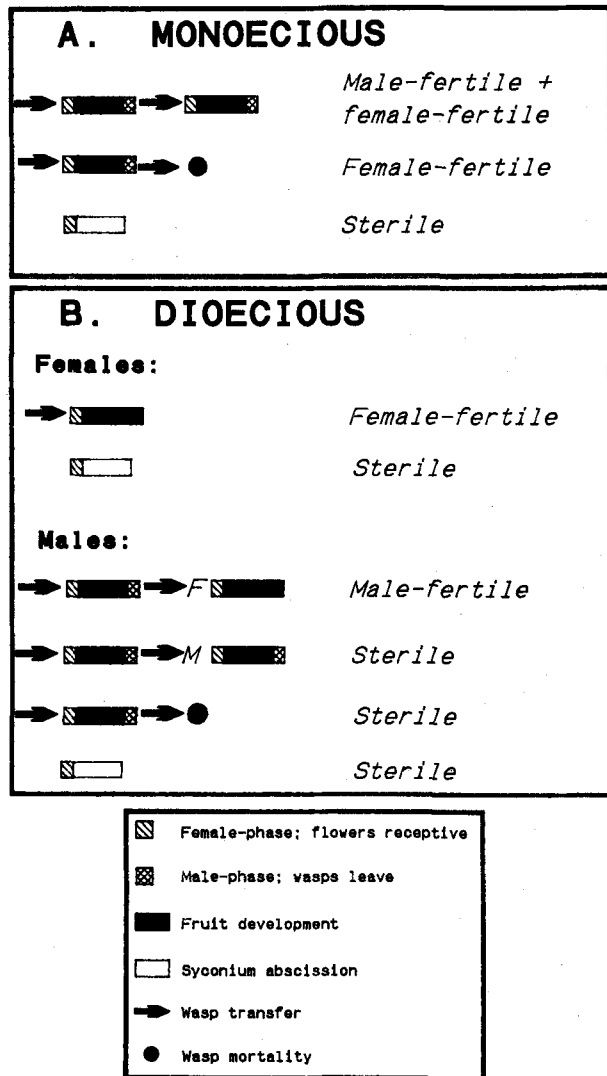
Figure 2. Possible outcomes of reproductive cycles for (A) monoecious figs and (B) dioecious figs.

A. MONOECIOUS

1
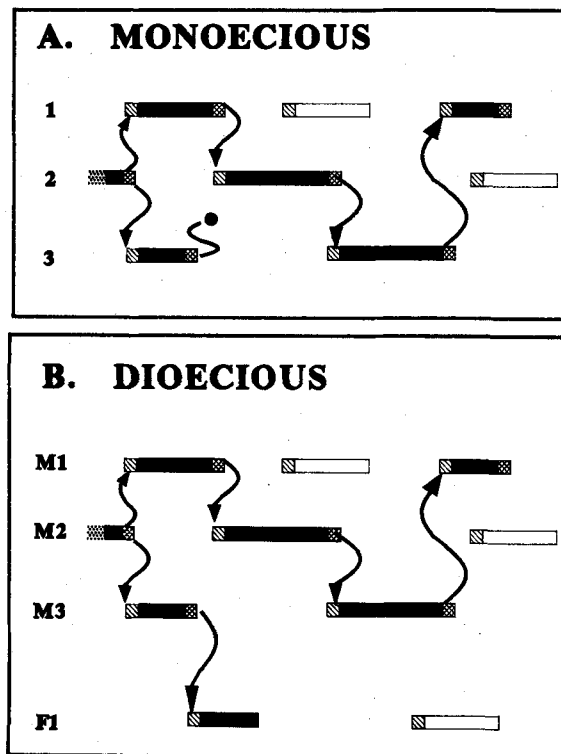
2

3

B. DIOECIOUS

M1

M2

M3

F1

Figure 3. Models of the fig/pollinator interaction at the population level, for (A) monoecious figs and (B) dioecious figs. Symbols used are the same as in figure 2, and are defined there.

set by a complex interaction among fig traits (such as syconium number and size), wasp traits (including fecundity, ovipositor length, and oviposition strategy), and parasitism [3, 5, 15, 17, 27, 41, 51, 65, 74, 85, 87].

Bronstein et al. [21] used repeated stochastic simulations of the phenological model shown in figure 3 a to identify the factors determining whether an individual crop within a monoecious fig population would attract pollinators. Assuming that all times of year were equally good for flowering (but see below), they showed that the critical variable was the number of crops in male phase per week, which increased with population size/(mean crop duration + mean interval between crops). Each of these variables is likely to be affected by seasonality in such a way as to decrease the frequency of male-phase crops, and hence of successful pollination events. First, durations of fig reproductive episodes are longer in cooler weather because seeds and wasps develop more slowly then. This

is clear, for instance, when one compares the average duration of a F. sycomorus cycle between a site in Namibia [118] and sites in Kenya 20° further north [47]. The same effect can be seen within individual populations in seasonal environments: the Elisabethiella wasps associated with F. burtt-davyii develop 5–7 days more slowly during the cool season in South Africa [3]. Similar data do not exist that would allow between-crop intervals of one species to be compared between sites or seasons, but it seems reasonable that intervals would be longer in cool habitats marginal for figs; interval probably increases as accumulation of resources necessary for reproduction slows [88]. Finally, if crop durations and intervals are longer in seasonal environments, leading to more frequent crop failures, seed production and ultimately population growth should be lower as well. Population sizes will also be constrained in semitropical habitats by the lower availability of the relatively specialized germination and establishment sites required by many tropical fig species [86, 96, 106].

A major difference between seasonal and aseasonal environments for figs should be the suitability of different times of year for flowering, seed production, seed dispersal, and germination. In equatorial Gabon, a nearly aseasonal habitat, Michaloud [85] has found flowering in a F. natalensis population to be almost evenly spread through the year. In contrast, nonequatorial fig species show distinct seasonal rhythms in phenolo-

gy [2, 3, 68, 88, 89, 92, 118, 125]. For example, two Panamanian species (*F. insipida* and *F. yoponensis*) consistently fruit more often towards the beginning and end of the rainy season, and less often in mid-wet season and late dry season [88]. The proximate factors leading to these flowering rhythms are as yet unknown, but their ecological consequences would seem clear. The probability of successful pollination for figs and survival for wasps should be much lower during periods when few trees in the population are in a reproductive phase [21]. If such rhythmicity were strong enough to create seasonal gaps in the flowering sequence, fig reproduction and wasp survival would clearly be impossible: wasps emerging during the gap would die off, and no tree within the population could reproduce again until wasps recolonized during a better season.

Factors determining the success of searching wasps
The simple phenological model in figure 3a (as well as the simulations of it by Bronstein et al. [21]) assumes that if the male phase of one tree corresponds to the female phase of another, then successful wasp transfer will always occur. However, it is critical whether or not a given tree is in fact releasing a clear and detectable signal during its female phase that searching pollinators can use successfully. This is determined by an interaction of fig and wasp traits, notably the nature and intensity of the figs' signal and the searching behavior of the wasps. All are likely to be sensitive to temperature, wind and humidity.

Presence of an effective attractant. Patterns of pollinator arrivals to fig trees suggest that a tree is attractive to searching wasps only very briefly. Pollinator entry into syconia often occurs over a period of only a few days [16, 89, 94, 118]. Bronstein [16] used sticky traps on and near *F. pertusa* trees in Costa Rica to investigate whether this arrival pattern reflected the brief presence of some attractant, or was simply another manifestation of the varying availability of searching pollinators. Three observations supported the first hypothesis: 1) pollinators arrived during a brief period coinciding with the presence of unentered syconia; 2) in one case peak arrivals occurred several days *after* peak departures from another tree only 40 meters away; and 3) pollinators directly introduced to the receptive tree readily entered syconia well before natural arrivals began.
These arrival patterns suggest the existence of a long-distance olfactory, rather than visual, attractant for pollinators. Olfactory cues have long been seen as the only logical way that figs could reliably attract large numbers of the minute pollinators from long distances at the appropriate moment [29, 74, 94, 108]. Evidence for such cues is still largely circumstantial, although research into them is progressing rapidly. Glandular and nonglandular trichomes on the syconial surface that are probable sources of aromatic compounds have been located [1, 4]. An odor can be detected emanating briefly from receptive *F. carica*

syconia [29, 108], and the one study to use gas chromatography has detected a volatile substance released at about this point in *F. ingens* [6]. No investigations of wasp behavior in response to such volatiles have yet been attempted, however, and thus their mode of function, as well as their frequently assumed species-specificity, remain hypothetical.
Once an effective assay for the attractant is developed, it will be possible to investigate whether variation in its strength and detectability might explain part of the great variation in pollinator arrivals. The number of arrivals to different *F. pertusa* crops within one Costa Rican population was surprisingly predictable on the basis of average syconium size at the moment of receptivity, suggesting that the strength of the attractant may vary according to when, during the period of syconium expansion, it is released [17]. Variability both within and among populations may also be related to climate. Both the production rate and diffusion rate of plant volatiles are highest on sunny, warm days [124]. Odors disperse more rapidly in windy conditions, becoming less detectable to small airborne insects [24].

Response to the attractant. How fig wasps search for syconia and how far they travel when doing so is very poorly understood. In fact, almost nothing is known about what happens to them after they leave their natal trees.
It is clear that fig wasps have the *potential* to travel long distances between trees. For example, the pollinators of the planted Asian ornamentals *F. rubiginosa* and *F. racemosa* were introduced into Oahu in 1921, and by the 1930s had arrived on their own to another island 100 km away [93]. Ramirez [94] found that isolated fig trees in city parks in San Jose, Costa Rica occasionally attracted pollinators even though the nearest conspecific individuals were several kilometers away.
Exceptional cases of long-distance wasp travel to isolated trees are actually much easier to document than *typical* travel distances, but they should not be overinterpreted. Rare long-distance flights should be critical for the establishment of isolated, reproductive fig populations, and will counter local genetic differentiation within them. But is is the flight distance of the average fig wasp that determines whether trees will be well-visited. As yet that distance is unknown. To the extent that we do know, however, they generally fly the shortest distance possible. Data are available for only one species, *Blastophaga psenes,* the pollinator of *F. carica* (a dioecious species that produces the edible fig). The behavior of this wasp has been studied recently in southern France using mark-recapture techniques. When *B. psenes* emerge from syconia on male trees in May, there are receptive syconia both on that same tree and on neighboring male trees. They nearly always enter a syconium on their natal tree within 50 cm of their natal syconium [81]. When the offspring emerge from those syconia in July, they must move to

female trees, and they generally go to the receptive individual that is nearest[79].

While data from more species are obviously needed, it makes sense that the wasps should travel the shortest possible distance. The closest receptive syconia must usually be the strongest source of the putative chemical attractant. Furthermore, there must be enormous risks to wasps in flight. I estimate that in Costa Rica, about one million fig wasps leave the average *F. pertusa* tree but only about 50,000 (one in 20) arrive. Herre[65] calculates an even lower success rate for Panamanian fig wasps. Free-living fig wasps are common in the diets of ants, dragonflies and birds; these and other predators descend on fig trees as the wasps arrive and depart[19, 27, 67, 74].

Vagaries of climate are also likely to influence survivorship and behavior of these small insects. Joseph[78] cited a longevity of 2–3 days for *B. psenes* held in the laboratory, whereas Grandi[60] kept several individuals alive for 4–5 days and Vallese[112] for eight days (see also Baijnath and Ramcharun[2, 3]). Lifespans in the wild have been thought to be much shorter, possibly only hours[28, 74]. So far the only field data are those of Kjellberg et al.[81] for *B. psenes*. None of the estimated 75,000 wasps they marked was recaptured entering a syconium more than two days after departing the natal tree (although it is of course possible that they could have lived longer, had they not found a receptive syconium). It remains to be seen whether this brief lifespan is typical for fig wasps, or even for *B. psenes* in different climates. Some evidence for the importance of environmental conditions can be gleaned from Pemberton's[92] laboratory studies of *Pleistodontes froggattii*, the pollinator of *F. macrophylla*. Fourteen percent of 200 individuals held in the dark lived longer than two days, whereas under light conditions, none did. When chilled to 10 °C, many survived for two weeks; upon warming up, they successfully entered syconia on trees to which they were introduced. Under more natural conditions, climate will affect behavior as well as longevity. Insects that use olfaction to find plants are in general either less responsive to or have more difficulty tracking odors in the cold and in windy conditions[13, 25, 38, 62]. Fig wasps will not fly in either the hot summer afternoon or on cool mornings in southern France[79]. Problems of fig wasp flight and survival in the cold have been assumed to be a major ecological factor restricting this mutualism to the tropics.

Summary: Problems at the edge of the range
In summary, two general problems should limit the success of the 'typical' fig pollination mutualism in markedly seasonal environments. First, trees will flower more rarely at some times of year, decreasing the success of searching pollinators. Secondly, trees that do flower during the harsher season will be less likely to be found, either because they are less detectable or because of high wasp mortality in flight. Both factors make it difficult for pollinator populations to persist locally.

The net effects of these constraints can be illustrated by comparing the ecology of one species, *F. sycomorus*, at four sites: Gobabeb, Namibia (23°34' S)[118], Magadi, Kenya (2°08' S)[47, 50, 51], Cairo, Egypt (30°03' N)[22], and Tel Aviv, Israel (32°05' N)[48]. The natural distribution of *F. sycomorus* includes the eastern coast of Africa from South Africa to Sudan, along stream banks and other sites where the water table is high; whether or not it is native to the Middle East is debated[57].

Two relevant observations emerge from this comparison. First, the pollinator (*Ceratosolen arabicus*) is present in Kenya and Namibia (and throughout Africa[57]), but absent in the Middle East. Archaeological evidence indicates that *F. sycomorus* has been artificially propagated there possibly for as long as ten thousand years[47, 57]. Secondly, while flowering within a tree is highly synchronized at all locations, the population-level flowering pattern is strikingly site-specific. Galil and Eisikowitch[47] imply that in Kenya, where there are no seasonal or diurnal temperature extremes (fig. 4d), some portion of each population is in flower at all times of year. In central Namibian forests, Wharton et al.[118] observed fewer trees in reproductive phase during the winter (July–September). In contrast, *F. sycomorus* is nearly dormant during the Israeli winter, when temperatures can fall below zero (fig. 4a); syconia are initiated only rarely, and those few develop very slowly[48].
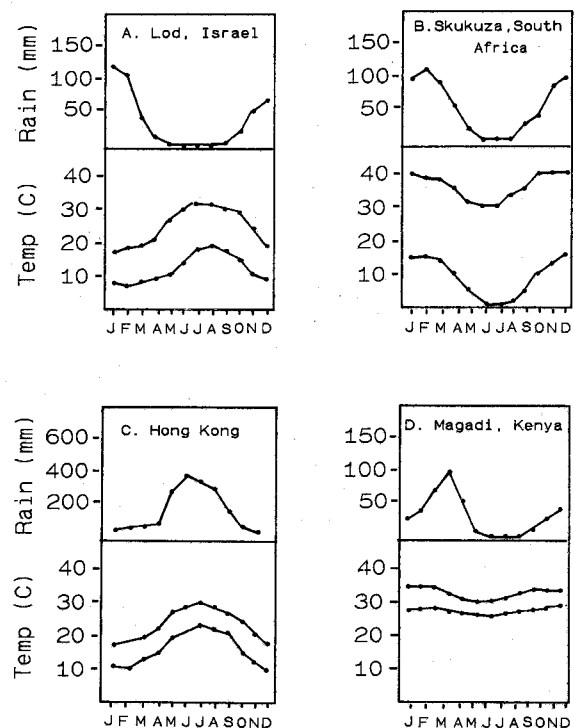

Figure 4. Climatic data for four sites with reproductive fig populations (see text and Appendix). Three sites (*A–C*) experience strong temperature fluctuations, and one (*D*) does not. Average monthly rainfall, average daily maximum temperature, and average daily minimum temperature are shown. *A*, *B*, and *D* are redrawn from[57], and *C* is redrawn from[68].

This flowering gap helps to account for the absence of the pollinator of *F. sycomorus* in the Middle East. Low winter air temperatures should make flight very difficult in any case. However, Galil et al.[57] believe other factors must be involved as well, pointing out that *F. sycomorus* pollinators apparently do persist in Kruger Park, South Africa, which occupies a southern latitude analogous to the Middle East and experiences even greater temperature extremes (fig. 4b). Comparative studies at this site would be illuminating. It should also be pointed out that the pollinator of the introduced fig *Ficus religiosa* has invaded and persist successfully in Israel[49].

Adaptations to seasonality

Despite the easily identified difficulties for the fig-pollinator interaction in seasonal environments, some species clearly do persist and reproduce successfully where temperature fluctuations are considerable (fig. 4). Fig biologists believe that seasonality must in these cases have selected for adaptations allowing the pollinators to persist during the winter months.

The synchrony-breakdown hypothesis

Most monoecious fig trees (or at least, most of those studied to date) initiate syconia synchronously and then attract pollinators for a few days at most. Ramirez[94] and Janzen[74] suggested that fig wasp populations could persist during harsh seasons if at least some emerging females could enter receptive syconia on their natal tree, rather than having to leave in search of another. They therefore hypothesized that these conditions should select for a breakdown in within-tree reproductive synchrony. At least six species (some of which occur in mar-

ginal habitats) have in fact been observed to have syconia in different stages of development on a single tree (table 2). Below, I evaluate the evidence for this synchrony-breakdown hypothesis, which seems recently to have risen nearly to the status of fact.

Are crops sufficiently asynchronous to allow within-tree wasp transfers? Crop asynchrony would only eliminate the need for long-distance wasp flights if asynchrony were great enough that male phase (wasp-releasing) and female phase (wasp-attracting) syconia occurred on the same tree. Unfortunately, published information on crop asynchrony is anecdotal, making it impossible to judge whether the observed levels of asynchrony would be sufficient to allow within-tree wasp transfers. For this reason, Sandrine Maurice, Aviva Patel and I have made quantitative measurements of crop asynchrony in the native Florida fig species. Casual observations by ourselves and others[23, 94] indicate that throughout south Florida, *F. citrifolia* (fig. 5) and *F. aurea* (fig. 6) often bear syconia in many stages of development. During the late spring of 1988, we examined three or more haphazardly chosen branches of seven *F. citrifolia* and 10 *F. aurea* trees on and near the University of Miami campus in Coral Gables. Syconia were dissected and classified into the developmental phases defined by Galil and Eisikowitch[47] (table 1). Our results are shown in table 3 (*F. citrifolia*) and table 4 (*F. aurea*). They can be summarized as follows.

1) In both species, the level of within-crop asynchrony differed among trees in a given week, from completely synchronized (*F. aurea* #6, table 4), to highly asynchronous (*F. citrifolia* #7, table 3).

Table 2. Monoecious fig species with asynchronous crops on individual trees. Introduced species are starred.

Species	Site		Published description or observation	Reference
F. aurea	San Andres Island, Colombia	2°32′ N, 81°42′ W	Syconia in all phases of development	94
	Coral Gables, Florida, USA	25°43′ N, 80°16′ W	see table 4	this study
F. citrifolia	Coral Gables, Florida, USA	25°43′ N 80°16′ W	see table 3	this study
F. burtt-davyii	Durban, South Africa	29°50′ S, 31°00′ E	Initiation staggered over 3–4 wk; trees always have at least a few syconia	3
F. microcarpa	Hong Kong	22°11′N, 114°10′ E	Many trees with continuous production; most in one size class with a few in between	68
	Singapore	1°17′ N, 103°50′ E	Most trees with a few syconia at various stages of development most of the time	30
	Tzitzio, Mexico*	10°34′ N, 100°44′ W	Continuous development	Ramirez, pers. comm.
	Coral Gables, Florida, USA*	25°43′ N, 80°16′ W	Some trees with branches at a different phenological stage from the rest of the tree	J. Bronstein and S. Maurice, unpubl. data
F. religiosa	Delhi, India	28°20′ N, 80°16′ E	While one crop of fruits is developing, the next one is initiated	77
F. sur	Durban, South Africa	29°50′ S, 31°00′ E	More asynchronous in summer, when more trees in flower; Subsequent crops initiated before one crop has finished its developmental cycle	2
	Harare, Zimbabwe	17°43′ S 31°05′ E	Individual trees often have syconia at different stages of development	37

Figure 5. A particularly asynchronous branch of *F. citrifolia* (Coral Gables, Florida, USA). All the developmental stages defined by Galil and Eisikowitch[47] are present (relative syconium size is an accurate reflection of developmental stage).
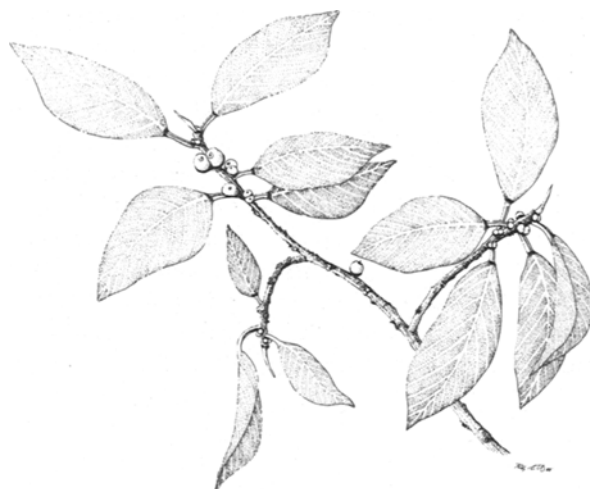

Figure 6. A particularly asynchronous branch of *F. aurea* (Coral Gables, Florida, USA). All the developmental stages defined by Galil and Eisikowitch[47] are present (relative syconium size is an accurate reflection of developmental stage).

2) The level of synchrony also varied over time for individual trees. Some changed from completely synchronous to highly asynchronous during the seven-week study (*F. citrifolia* #1, table 3).

3) Even in asynchronous crops, we rarely observed overlap between the brief female phase (B) and male phase (D) which would allow within-tree wasp transfer to occur. Somewhat more often we saw overlap between the long phases A (pre-female) and C (interfloral), or between C and E (postfloral), indicating that B and D phases may have overlapped on these trees before or after our census dates.

Thus, crop asynchrony occurs very patchily in time and space, and only occasionally is sufficient to permit within-tree wasp movements. Further studies are needed to determine whether these species are typical among those with crop asynchrony.

Is crop asynchrony more common in the winter? The synchrony-breakdown hypothesis is often interpreted to imply that synchrony should break down only during the harshest season, when the risks of between-tree wasp transfers are the greatest. Crop asynchrony would, it is assumed, be at a selective disadvantage at other times of year; if fig wasps do fly the shortest distance possible, they would, if given the opportunity, never transfer pollen between trees.

The limited data available strongly refute these assumptions. Baijnath and Ramcharun's[2,3] studies of *F. sur* and *F. burtt-davyii* in South Africa show clearly that asynchronous crops are actually most common in the warm rainy season, when the largest proportion of trees are in reproductive phase. We have not yet studied the phenology of the Florida figs in winter, but it is clear that crop asynchrony is very common during the favorable, warm spring, as well as in autumn (J. Bronstein, unpublished data). Nearly all fig trees we saw during our study were in reproductive phase.

Table 3. Crop asynchrony within Florida *F. citrifolia* trees. Proportions of syconia in each developmental phase (see table 1) are given.

Tree	Date	Sample size Bran-ches	Sample size Sy-conia	A	B	C	D	E
1	5/3	5	148	0.57		0.34	0.05	0.04
	5/19	5	60	0.06	0.57	0.30	0.02	0.05
	5/24	12	100			0.94	0.02	0.04
	6/3	11	100			0.96		0.04
	6/14	5	60			0.58	0.27	0.15
2	5/4	5	36			1.00		
3	5/2	5	41	0.27	0.12	0.32	0.07	0.22
4	5/4	3	67			1.00		
5	5/1	5	78	0.54	0.26	0.20		
	5/18	5	50			1.00		
	5/25	5	100			0.99	0.01	
6	5/23	5	36	0.19	0.17	0.64		
	6/9	5	64	0.23		0.66	0.11	
7	5/23	5	30	0.10	0.07	0.30	0.10	0.43
	6/9	5	30	0.43	0.10	0.44	0.03	

Table 4. Crop asynchrony within Florida *F. aurea* trees. Proportions of syconia in each developmental phase (see table 1) are given.

Tree	Date	Sample size Bran-ches	Sample size Sy-conia	A	B	C	D	E
1	5/6	5	39	0.49		0.38		0.13
2	5/6	5	38	0.42		0.58		
	5/29	5	40	0.52				0.48
	6/14	5	47	0.89				0.11
3	5/30	4	89	1.00				
4	4/30	5	48			1.00		
	5/31	5	27	0.15		0.18	0.07	0.59
5	4/29	5	94	0.17		0.53	0.08	0.21
	5/30	5	57	0.84	0.02			0.14
	6/14	5	65	0.98		0.02		
6	5/29	5	30	1.00				
7	5/29	5	78	0.78		0.01	0.03	0.18
	6/15	5	55	1.00				
8	5/31	5	35	0.94				0.06
9	5/31	5	32	0.56		0.18		0.25
	6/14	5	42	0.93		0.05		0.02
10	6/5	4	97	0.98				0.02

Thus, evidence to date indicates that the probability of within-tree wasp transfers is actually greatest during the best, not the worst, times for long-distance flights.

Do most monoecious fig species in seasonal environments show crop asynchrony? If wasp flight is constrained in winter, species with asynchronous crops should be at a selective advantage in seasonal habitats. No surveys have yet been attempted to compare the proportion of fig species having asynchronous crops between seasonal and aseasonal sites. However, two observations call into question this hypothesized advantage. First, in the only community-level survey at a seasonal site, Hill[68] found crop asynchrony in only one of the five native Hong Kong species. For *F. microcarpa* var. *microcarpa*, he notes that 'in most cases there was continuous production of fruit throughout the year both by the species as a whole and by many individual trees. It was quite common to find all stages of fig developing on any one tree at the same time, although the bulk of the crop was usually in one or two size categories'. In contrast, Hill lists the other species (*F. superba* var. *japonica*, *F. virens* var. *sublanceolata*, *F. vasculosa* var. *vasculosa*, and *F. nervosa* var. *nervosa*) as having non-overlapping, 'well defined' or 'sharply defined' crops. All five species reproduced successfully. The second observation is that some species with asynchronous crops do occur and reproduce successfully in relatively nonseasonal environments. These include *F. microcarpa* in Singapore[30], *F. aurea* in Colombia[94], and several species in Costa Rica, Peru, Borneo, and tropical Australia (J. Bronstein, C. Janson, L. Curran, and J. Addicott, pers. obs.).

Thus, successful species with synchronous as well as asynchronous crops can be found throughout the range of the genus. Further studies will be necessary to determine whether species with asynchronous crops might be proportionally more common at the edge of the range.

Does the level of crop synchrony vary across the range of a single species? If seasonality selects for a 'breakdown' in crop asynchrony, as Ramirez[94] and Janzen[74] suggest, we might expect species with large ranges to have asynchronous crops at seasonal sites and normal, synchronized ones elsewhere. However, no monoecious species has yet been identified that has a different level of crop synchrony in different parts of its range. Consider *F. microcarpa*, an Australasian species of New Guinea origin that has an exceptionally large natural range (from 30° N to 30° S)[32]. In the relatively seasonal conditions of Hong Kong *F. microcarpa* bears asynchronous crops. It also has asynchronous crops in the aseasonal climate of Singapore (1°17' N): Corlett[30] found that 'the majority of plants carried a few syconia at various stages of development most of the time.' Introduced trees in Florida (J. Bronstein and S. Maurice, unpubl. data) and Mexico (W. Ramirez, pers. comm.) also bear asynchronous crops. Conversely, *F. sycomorus* has highly synchronous

crops throughout its range, although this is clearly disadvantageous in the seasonal climate of Israel.

Current evidence therefore suggests that species either have synchronous or asynchronous crops; the level of synchrony is not habitat-specific.

What is crop asynchrony? Many fig biologists now believe that crop asynchrony is far more common than the number of records would indicate. But at this point, there is no clear evidence that it is an adaptation evolved in the context of seasonal conditions. The geographical distribution of crop synchrony and asynchrony is not in accord with this hypothesis (although this may be due to incorrect assumptions about what contitutes a harsh season; see below). Moreover, both the hypothesized benefit and cost of crop asynchrony seem doubtful. Situations in which such asynchrony occurs in winter *and* is sufficient to allow within-tree wasp transfers (its presumed benefit) do not seem very common. Self-pollination (its presumed cost) may not be a great risk: crop asynchrony is often greatest during the best season for outcrossing, and some species with asynchronous crops are common and successful in aseasonal habitats.

I would suggest that the benefit of asynchrony is not that it very occasionally allows within-tree wasp transfers, but that it always prolongs the period over which wasps arrive and depart from the tree. Trees would experience two advantages of such extended female and male phases: the chance of a 'match' with the opposite sexual phase of a neighbour would increase (fig. 3a), and the chance that some syconia would be in male or female phase on a day that was favourable for wasp flight would increase. The biggest disadvantage of having asynchronous crops may be a low detectability to pollinators: cumulatively, the attractant released by receptive syconia should be much weaker than in synchronous crops. Tests of these costs and benefits should involve 1) precise measurements of the level of crop asynchrony; 2) mark-recapture experiments designed to show whether wasps do stay on their natal trees when possible; 3) examination of syconia entered by those wasps, to measure the consequences of self-pollination; and 4) measurements of pollinator attraction success to see if it is a function of crop asynchrony. We have recently begun these studies on the Florida figs (J. Bronstein and A. Patel, unpubl. data).

Thus, two pollinator attraction strategies may exist: attracting many pollinators in highly unpredictable bursts, or attracting them continually and more reliably but in much lower numbers. This latter trait may explain why species with asynchronous crops seem common in marginal habitats: crop asynchrony should preadapt them to be good colonizers, because when the male and female phases are greatly prolonged, a local wasp population requires fewer trees to persist. Broad surveys of phenological traits in isolated but reproductive populations in nonstressful habitats would clearly be of value. For example, crop asynchrony may partially account for

the success of *Ficus microcarpa* as an invading species. Its pollinator has rapidly become established on ornamental trees in many parts of the New World, following some inadvertent and undocumented introductions (R. J. Knight, D. Hilburn and W. Ramirez, pers. comm.). Small populations of many other Asian and African fig species exist at the same locations, but almost none of them are associated with their pollinators. While it is possible that only the pollinator of *F. microcarpa* has yet appeared in the Western Hemisphere, it may also be that this wasp has been uniquely able to persist in small populations because of *F. microcarpa*'s marked crop asynchrony.

The specificity-breakdown hypothesis

Janzen[74] proposed that one-to-one specificity between fig and pollinator species might also break down on islands and in harsh environments. He reasoned that long-distance seed dispersal events must often extend figs' ranges into areas in which their pollinators have not reached or cannot reach[79, 100, 110]. Fig wasps endemic to those marginal areas would generally have few of their own mutualist partners both present and flowering regularly. A breakdown in specificity (involving selection on wasps for latitude of fig choice and selection on the invading fig species for retention of syconia receiving some wrong pollen) might then be in the selective interests of both species. The example Janzen[74] offered in support of his hypothesis involved pollinator-sharing between *F. aurea* and *F. citrifolia* in south Florida, their northern range limit. However, the supposedly shared wasp, *Secundeisenia mexicana* Ashm.[23], has recently been separated by J. T. Wiebes into two species: *Pegoscapus jimenezi* Grandi (associated with *F. aurea*) and *P. assuetus* Grandi (associated with *F. citrifolia*)[123].

If the specificity-breakdown hypothesis were correct, we would expect to find some exceptions to species-specificity in which (fig. 7): 1) one fig species (A) is usually associated with fig wasp a, but is found with fig wasp b in the harsher or more isolated part of its range; and 2) at that location, fig wasp b is associated with both fig A and another fig species, B. I know of no cases meeting both criteria. Exceptions to specificity that meet one of the two criteria are well documented[87, 119, 121, 122]. However,

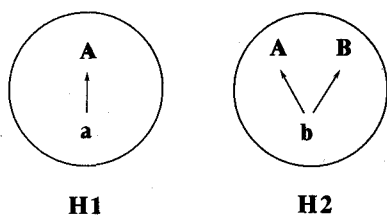**H1**   **H2**

Figure 7. A schematic diagram of the specificity-breakdown hypothesis (see text). H1 and H2 are disjunct habitats; capital letters are fig species and small letters are the fig wasps that pollinate them. When fig A invades a habitat (H2) that its pollinator (a) cannot reach, selection may act to break down the specificity of the endemic interaction between B and b, leading to pollinator-sharing between A and B.

there is generally no information on whether one of the two habitats in question is harsher or more isolated than the other, and mechanisms other than the one suggested by the specificity-breakdown hypothesis can be identified that could account for the absence of specificity in each case[87]. The situation that comes closest to fulfilling both the criteria of the specificity-breakdown hypothesis is one described by Corner[33]. *F. obliqua* (section Malvanthera) in Fiji 'should' be pollinated by *Pleistodontes imperialis*, as is *F. obliqua* var. *petiolaris* in Australia. In fact, it is pollinated by *Blastophaga greenwoodi*[120]. Corner[33] suggests that the ancestor of *B. greenwoodi* was shared between the invading *F. obliqua* and one of the many common indigenous species of *Ficus* section Sycidium, which are usually associated with the genus *Blastophaga*. Pollinator-sharing would have led to isolation and then sympatric speciation among the wasps.

Although at this point the specificity-breakdown hypothesis has little empirical support, it should be pointed out that there are two fundamental difficulties with using existing data to test it. First, identifications of pollinators are frequently made from collections taken at very few sites, and populations in marginal habitats are usually not the ones sampled. Therefore, exceptions to specificity in these locations, and for that matter other cases of geographical variation in specificity, will generally be missed. Secondly, the common belief that the mutualism is virtually always species-specific has probably prevented exceptions to specificity from being recognized and acknowledged. For example, although Hill[69] had observed that *F. pyriformis*, *F. variolosa*, and *F. erecta* var. *beecheyana* were pollinated by the same wasp in Hong Kong, he concluded that there must actually have existed three morphologically indistinguishable species. These two difficulties suggest that exceptions to specificity in marginal habitats will only be found by explicitly looking for them there.

Some alternative hypotheses

Adaptations of fig wasps. All the adaptations to seasonality that I have discussed so far are adaptations of fig trees. However, it may be more reasonable to look for such adaptations among the fig wasps. Selection on the wasps should be much stronger; an inability of the wasp to reach a fig in winter leads to reduced reproduction in one of many attempts for the fig, but leads to death for the wasp. The effects of such selection on wasps should also appear more rapidly, since they undergo perhaps 300 generations to each generation of the fig. Moreover, wasp populations adapted to seasonality would experience lower gene flow from populations in aseasonal environments, because fig wasps probably migrate shorter distances than fig seeds do[74, 110] and show extremely high levels of inbreeding[43, 61, 64].

Studies comparing the characteristics of different fig wasp populations will be necessary for identifying habitat-related adaptations of free-living wasps. Fig wasp

species do vary in color, diurnal or nocturnal habit, size, and habitat preference[52, 65, 87, 95], suggesting that adaptations to different environmental conditions do exist. Behavioral and physiological adaptations for flight in cool weather are well documented in insects[70, 97, 117]. *Drosophila melanogaster* populations, for example, are differentially adapted to temperature and desiccation stress along ecological gradients in Australia[90, 91, 103].

Plasticity of developmental time. The ability of syconia to mature more slowly, yet successfully in cool conditions deserves attention as another mechanism allowing the mutualism to persist in some seasonal environments. For example, Hill's[68] data from Hong Kong indicate that winter crops of most monoecious species took almost twice as long to develop as summer crops did, and as a result wasp emergences were rare or absent during the coolest months of December-February. Maturation time is apparently set by an interaction between fig and wasp traits[58], and developmental rates of some (but not all) fruits[107] and insects[126] are temperature-dependent. To test whether delayed development does in fact increase the success of the interaction in winter, it will be necessary to determine whether 1) slower-developing wasps mature normally, 2) the delay does allow these wasps to emerge at a better time to locate receptive syconia, and 3) the syconia they enter in the spring develop normally. Models of Kjellberg and Maurice[30] suggest that seasonality should select for two kinds of trees within a population, one with syconia in which seeds and wasps develop slowly through the winter and one with syconia that reach receptivity in early spring. Such selection could lead to the evolution of dioecy.

A nonadaptive perspective. It is also possible that although figs can persist in the marginal habitats to which their seeds are sometimes dispersed, they simply don't reproduce very well there, due to rare immigration and frequent extinction of their pollinators. Because pollination success has so rarely been measured in fig populations and has never been followed over time or compared over the range of a fig species, this possibility cannot be ruled out. For example, wild *F. carica* trees can be found all along the Atlantic coast of France, although their pollinators are absent above 46° latitude. Further north, populations are maintained by seed rain from more southerly locations. Ultimately the northern limit of *F. carica* appears to be set by frosts, which kill the seedlings[108].

Seasonality and dioecious figs

I have primarily considered how climate might affect the reproductive cycle of *monoecious* figs and their pollinators. However, there are also about 350 Old World fig species that are functionally dioecious[9, 116]. Although the natural history of their interaction with pollinators is still very poorly known, it is clear that their sensitivity

and responses to seasonality are somewhat different from the monoecious fig/pollinator interaction.

As we have seen, in the monoecious fig species, all syconia contain both male and female florets. The female florets vary greatly in style length; the ovaries therefore vary in accessibility to the fig wasps because their ovipositors must be inserted through the length of the styles. Consequently, a mixture of seeds and wasps matures in each syconium[19]. In contrast, in the functionally dioecious species there are two kinds of trees, each with a distinct type of syconium. On female trees, syconia contain only female florets, and all of these are long-styled; therefore, female syconia entered by fig wasps produce seeds only. On other trees, syconia contain male florets and uniformly short-styled female florets; when these syconia are entered by fig wasps, they primarily produce pollen-carrying offspring. These latter trees are therefore hermaphrodites, and these species gynodioecious, but functionally they are (respectively) male and dioecious[109, 116]. I will use the latter terminology, in accord with most current literature on figs.

Because there are two kinds of trees in dioecious species, the three outcomes of a reproductive cycle shown in figure 2a are not applicable. There are now six possible results (fig. 2b). If a female tree attracts wasps, it will be female-fertile, and if it does not it will be sterile. If a male tree attracts wasps and the offspring of those wasps successfully reach a female tree, it will be male-fertile. But if a male tree either 1) attracts no wasps, 2) attracts wasps, but their offspring can reach no other tree, or 3) attracts wasps, but their offspring reach only male trees, it will be sterile. However, the *wasps* can only reproduce by transferring between male syconia. The potential for conflicts of interest between wasps and dioecious figs is clearly great, and the complex evolutionary consequences have only begun to be explored[81, 109]. But the critical point here is that for a local wasp population to persist year-round, wasps must always be developing on some male trees (fig. 3b), not just on any tree, as was the case for monoecious figs (fig. 3a).

What sort of population-level flowering patterns emerge? Quantitative data are available for only two dioecious species, *F. fistulosa* and *F. carica. F. fistulosa* was studied recently by Corlett[31] in aseasonal Singapore. Corlett censused six female and 11 male trees at one- to three-week intervals for 14 months. He found that crops on individual trees were highly synchronized, but different trees flowered out of synchrony. Wasps were always developing on some male tree in the population. Wasp transfers could have occurred in 86% of all two-week periods, with the possibility of male-to-male transfers frequent enough to allow the local wasp population to persist throughout the study period.

Climatic variation has two effects on the phenology of *F. fistulosa*. First, in seasonal environments flowering becomes synchronized within sexes. In Hong Kong, each sex bears syconia at predictable times of year, with fe-

males consistently initiating crops two to four weeks after the males[68]. Secondly, as in some other dioecious species[31], *F. fistulosa* trees have fewer reproductive cycles per year in more seasonal environments (5–7 in Singapore versus 3–4 in Hong Kong). This is a consequence both of longer intervals between crops and of slower development of syconia.

The complex flowering phenology of *F. carica* has been studied extensively in southern France, one of the most extreme environments in which figs reproduce successfully[79, 81, 108–110]. Throughout its range (even where introduced as an orchard tree), *F. carica* females flower relatively synchronously within and among trees, whereas males bear syconia in a variety of stages most of the time. Several well-defined periods of wasp transfer occur, either from male to female trees, male to male trees, or male to male syconia on the same tree. The number of wasp transfers (hence, effectively, the number of reproductive episodes for individual trees) decreases progressively in cooler climates, until there are too few to allow the wasps to persist on trees year-round[81, 110]. Climate has this effect in part because the wasps develop far more slowly in cool conditions[110]. In addition, *F. carica* shows two notable adaptations to its seasonal environment[108]. First, only wasps, not seeds, develop through the winter, in particularly thick-walled syconia. Secondly, the next crop of male syconia is actually initiated in autumn; syconia can remain in an arrested stage of development all winter, and then rapidly reach receptivity as the overwintering wasps emerge.

It seems evident from these limited phenological data that seasonal climatic variation should be less of a problem for the mutualism in dioecious figs than in monoecious figs. Dioecious figs can better take advantage of any seasonal differences in conditions good for seed production and dispersal, and conditions good for wasp production and dispersal: each tree specializes on only one function, and the mutualism still functions well with some degree of within-sex flowering synchrony. Wasps evidently develop normally during winter in the very slowly maturing male syconia, and as long as their first spring transfer is to other male syconia, it is not even essential that pollen remain viable through the winter. In addition, characteristics such as syconium developmental time, number of crops per year, and sexual synchrony appear to be quite plastic, potentially allowing dioecious species to exploit wide geographical ranges. Berg's[8] current data in fact suggest that in seasonal environments, dioecious figs are more common than monoecious figs, although more detailed work on fig biogeography is necessary before a conclusive test of this hypothesis can be made.

Conclusions

Studies of geographical variability in species interactions generate hypotheses about their ecological and evolutionary dynamics. Competition studies in particular have been spurred by the comparative approach. For instance, evidence that traits can evolve by character displacement arose from comparisons of populations in sites with and without putative competitors[82]. As I have shown here, comparing populations that differ in access to mutualists can likewise provide evidence for how traits thought to be central in these interactions have evolved. For example:

1) Geographical comparisons allow some evolutionary hypotheses to be examined critically. Studies of fig species in some extreme latitudes had identified two relatively rare traits, crop asynchrony and lack of fig/pollinator specificity. Although their presence at the edge of the range had suggested that they were adaptations to the rarity of pollinators in cool weather, geographical and seasonal comparisons within and among fig species do not support these hypotheses. Conversely, the geographical distribution of fig breeding systems lends support to growing evidence that dioecy is at a selective advantage in seasonal habitats.

2) Comparisons can reveal unexpected geographical variability, generating new hypotheses. For example, plasticity of developmental time may allow fig wasps to remain in the 'refuge' of the syconium during the winter. Traits of fig wasps, rather than figs, may be most likely to respond to environmental selection pressures, but geographical variability in the wasps has not yet been looked for.

3) Geographical comparisons can suggest other, more appropriate kinds of contrasts. For example, studies of the distribution of crop asynchrony indicate that this characteristic may reflect invasive ability, thus warranting comparisons between colonizing and noncolonizing species away from the edge of the range.

Geographical comparisons, however, are often only correlative, relying heavily on assumptions about causality. In this paper, I have often assumed (along with other fig biologists) that latitude reflects a measure of climatic stress that is biologically relevant for figs and fig wasps. This is undoubtedly an oversimplification[126]. In many tropical habitats there are great yearly fluctuations in humidity, which might have as strong consequences for the mutualism as does temperature variation in more extreme latitudes; survival and reproduction both of small insects[83, 91, 103] and of plants[11, 40, 72] are very sensitive to moisture availability. Many ecologists have found that actual evapotranspiration (AET), which measures moisture and solar energy simultaneously, is the index that best reflects the varying suitability of conditions for plants and the animals that exploit them[98, 102]. If AET had been used, for example, Magadi, Kenya (4°03′ S; fig. 4d) and Tel Aviv, Israel (32°05′ N; fig. 4a) would have been considered to be equally seasonal environments; that would alter conclusions about how *F. sycomorus* and its pollinator respond to 'seasonality'

(AET data from Thornthwaite et al. [104, 105]). Ideally, therefore, detailed observations and experiments should accompany geographical comparisons. In the present case, the proximate effects of climate on figs and pollinators need to be measured directly, and the costs and benefits of supposed adaptations to seasonality (e.g., crop asynchrony) should be quantified.

Nevertheless, biologists studying the fig/pollinator interaction have already exploited a much wider range of approaches than is yet common in mutualism research. The rapid proliferation of data and theory over the last 20 years is the best evidence for the value of that diversity.

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Coevolution of reproductive characteristics in 12 species of New World figs and their pollinator wasps

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Summary. 1) Figs (*Ficus*) and fig-pollination wasps (Agaonidae) are highly coevolved mutualists that depend completely on each other for continued reproduction. However, their reproductive interests are not identical.

2) The natural history of their interaction often permits the direct measurement of total lifetime reproductive success of the wasp and of major components of reproductive success for the fig.

3) Data from 12 monoecious species of New World figs (subgenus *Urostigma*) and their wasp pollinators (*Pegoscapus* spp.) indicate that fig fruit size (number of flowers per fruit), wasp size, and the number of foundresses that pollinate and lay eggs in any given fruit interact in complex but systematic ways to affect the reproductive success of both the wasps and the figs.

4) Different aspects of the interaction may work against the reproductive interests of either the wasp or the fig, or often, both. For example, in some species an 'average' foundress may only realize 25% of its reproductive potential due to the high average number of foundresses. However, that same crowding selects for more male-biased sex ratios in the wasps that reduce potential fitness gains through pollen dispersal for the fig. Nonetheless, the natural distributions of numbers of foundresses per fruit more clearly reflect the reproductive interests of the figs than of the wasps.

5) Generally, it appears that most of the fig species studied can be arranged along a continuum from those with physically small fruits that produce a relatively low proportion of viable seeds but are very efficient at the production of female wasps to physically large, relatively seed-rich fruits that are relatively inefficient at producing female wasps. The implications of these findings for the coevolution of figs and their wasps are discussed.

Key words. *Ficus*; figs; fig pollinating wasps; pollination mutualisms; coevolution; sex allocation; plant breeding systems.