Population biology of figs: Applications for conservation

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Summary. The flowering phenology typical of at least monoecious figs – intra-tree synchrony and inter-tree asynchrony – poses problems for persistence of the pollinator population, and hence of the fig population itself, when fig population size is small. Establishment and maintenance of a population of the short-lived, species-specific wasp pollinator require that the fig population include a critical minimum number of trees (critical population size: CPS). Below CPS, temporal gaps between flowering trees occur that are unbridgeable by the pollinator, leading to its local extinction. This has implications for conservation in two contexts: human-aided invasions of introduced fig/wasp pairs, in which initial populations of figs and/or wasps may be small, and the persistence of figs and wasps in fragmented forest, in which initially large populations may be drastically reduced. Long-distance range extension by fig/wasp pairs is problematical for two reasons: 1) the fig species must first attain CPS, most likely through repeated seed dispersal events, before the wasp can establish; and 2) long-distance transit should be difficult for the tiny, short-lived wasp pollinators. I review the biology of natural and human-aided range extension by figs and fig wasps, and show that in human-aided range extensions these two difficult steps are circumvented. Once introduced into an area where hosts are abundant, fig wasps should readily establish from a small number of initial colonists, since they mate before dispersal and are highly tolerant of inbreeding. They are thus less subject than many insects to the genetic and demographic hazards of small population size. Of 5–6 fig/wasp pairs that have performed human-aided long-distance range extensions, one Asian pair, *Ficus microcarpa* and its pollinator *Parapristina verticillata*, is established in numerous areas in the northern neotropics, and the plant may become a serious weed.

In tropical forests, figs may provide keystone resources for frugivores, providing fruit during seasons when other resources are scarce. Figs pose difficult problems for conservation biology, since minimum viable populations appear to be large, and since many species of tropical rainforests occur at low densities. This means that minimum areas required for persistence of a fig population – and for those of other species that would be affected were figs to be removed from the system – may often be large.

Key words. Ficus; fig; biological invasion; phenology; minimum viable population; conservation biology; keystone resource.

Introduction

There are two classes of situations in which it becomes important to manage populations of figs and their wasp mutualists. First, figs in fragmented natural forests may be important and endangered resources upon which many other species directly or indirectly depend, and whose persistence requires active intervention. Second, figs introduced into habitats outside their area of origin can sometimes be invasive weeds requiring control. The desired effects of management in these two cases are completely opposed, but the underlying biological problems are quite similar. In both these contexts, management centers around influencing, in one direction or the other, the establishment or maintenance of the pollination mutualism when population size of figs is small.

The unique reproductive biology of figs has important implications for life at low population size. Most monoecious figs, at least, are characterized by a combination of intra-tree synchrony and inter-tree asynchrony in flowering. When the pollen-carrying, inseminated female agaonids emerge from a tree's crop of fruits, they find no receptive figs on the tree from which they emerged, and are forced to find another tree with flowers at the appropriate stage. Coupled with the short lifespan of the species-specific pollinator, this phenological pattern means that a substantial number of reproductive individuals of a fig species must be present if its pollinating wasp, and ultimately the fig itself, are to persist.

Here I examine fig biology in two different contexts in which small population size of figs may pose problems for the maintenance of the mutualism. I first consider natural range extensions and biological invasions by figs and fig wasps. Here the problem is how the mutualism becomes established in a new area. This question is of practical importance because at least one species of fig, *Ficus microcarpa*, seems poised to join the ranks of the human-transported trees and shrubs that threaten to homogenize the tropics into a ragtag assembly of pantropical invasive species[44, 53, 65].

Secondly, I consider fig/pollinator mutualisms in fragmented forests. Here the problem is persistence of the mutualism in the face of great reduction in fig population size and increasingly restricted possibilities for interpopulation exchange of pollinators. In these circumstances, local extinction of the pollinator becomes more likely, as does failure of the fig population to be subsequently recolonized by wasps from neighboring populations. If figs are keystone resources for many wide-ranging frugivores, as some current work suggests[51, 80, 81], their extinction could have a devastating effect on biological diversity of tropical forest ecosystems.

Figs and fig wasps as invaders

Many species of figs have been widely planted as ornamentals in tropical and subtropical regions of the world. Introduced usually as seeds or small cuttings, they have lacked their species-specific agaonid pollinators in the area of introduction and have therefore been effectively sterile. Figs have consequently been considered 'safe' introductions[52], unlikely to escape cultivation and naturalize (i.e., self-perpetuate).

Unfortunately, agaonids have also been moved around, both intentionally and unintentionally. This has resulted in the establishment of a number of fig/wasp pairs thousands of kilometers outside their natural range. In some cases the trees seem well on the way to becoming naturalized, with juveniles soon to add to the population of reproductive adults.

How successful will figs and agaonids be as biological invaders? In this section I review first, the biology of invasion by figs and fig wasps, asking what data are required to predict invasion success, and second, the current status of introduced fig/wasp pairs. In many cases these invasions are little enough advanced that it is possible to study the process from a very early phase.

Natural range extensions by figs and fig wasps

There is much debate about what makes a good invader (e.g., Bazzaz[15] and Ehrlich[27]). Some workers despair of finding general principles. Simberloff[73] believes that the reasons for success or failure of a biological invasion reside in aspects of the particular species or system that are so idiosyncratic as to defy generalization. However, most workers would agree that examining the biology of the organism under study, in particular processes of natural range extension, is a good place to start.

Many students of figs, e.g. Corner[23], Hill[40], Janzen[42], and Kjellberg and Valdeyron[47] have noted the peculiar problems their biology poses for range extension via long-distance colonization. Fig and wasp are dependent on one another for reproduction, but disperse independently. Given the flowering phenology typical of monoecious figs, wasp colonists to a group of figs, e.g., on an isolated oceanic island, can only persist if numerous adult fig individuals are present. Until the wasps establish, though, the most likely way this threshold population size can be attained is by repeated long-distance dispersal of seeds from source populations.

The most likely scenario for long-distance range extension by figs thus seems to depend on a concatenation of unlikely events. The process may be divided into two components: 1) building up the number of adult fig trees required to sustain the wasps indefinitely; and 2) establishment of the wasps once enough host trees are present.

Attaining critical population size in figs. The first condition appears to be difficult, since before the wasps can establish, the fig population must attain a minimum number of adults. Rare long-distance dispersal of pollinators might lead to brief recruitment episodes in isolated fig populations (Bronstein, pers. comm.). Alternatively, recruitment must come from seed dispersal from other, seed-producing populations. Understanding this phase of range extension requires answers to two questions: 1) How many adult figs must be present to maintain a population of the pollinators? 2) How many independent events of seed dispersal does this require? In the first quantitative approach to a long-standing problem in fig biology, Bronstein et al.[21] asked how many fig trees were necessary to allow a wasp population to establish and persist. This minimum number of adult figs, the 'critical population' (CPS), will depend on fig phenological characteristics such as the degree of intra-tree reproductive synchrony, the interval between successive crops of an individual tree, and the distribution of crops over the year, as well as on the lifespan and flight capabilities of the pollinating wasps.

Using field data on phenology of *Ficus natalensis* gathered by Georges Michaloud[55] in Gabon, and incorporating biologically reasonable assumptions about wasp behavior and adult lifespan, Bronstein et al.[21] developed a stochastic simulation model to estimate the number of adult trees necessary to allow establishment of a wasp population and its persistence for 4 years. The median CPS was found to be 95 trees. In 100 runs of the model, CPS was quite variable, up to a maximum of 294 trees. Interspecific differences in phenology will affect CPS. The results of Bronstein et al.[21] point to the particular importance of interval between successive crops of an individual tree. In *F. natalensis* this interval averaged 44 weeks. As this interval is increased in the model, CPS increases. Interval between crops is highly variable among species, even at a single site[55], suggesting that fig species will be differentially effective as colonizers.

The best long-distance colonizers among figs, however, should be those in which each individual bears figs of all stages throughout the year. The model of Bronstein et al.[21] assumed intra-tree synchrony, as is typical of *F. natalensis* and most other monoecious figs. Janzen[42] suggested that departures from intra-tree reproductive synchrony, by permitting intra-tree transfer of wasps, would greatly decrease the number of trees necessary to sustain a wasp population. This suggestion remains unexplored quantitatively. Bronstein[20] proposes that species such as *F. microcarpa* exhibiting asynchronous crops may owe their broad distribution in part to this trait.

Bronstein et al.'s[21] model assumed random distribution of crops over the year, which seems to be the case in *F. natalensis*. Kjellberg and Maurice[46] present a somewhat similar model that explores the effect of seasonal variation in fig reproduction. The result is highly interesting: as flowering becomes more and more seasonal, CPS increases dramatically. For this reason, figs with highly seasonal reproduction should not be good long-distance colonizers.

Given that we can estimate CPS in a fig species, how many independent events of seed dispersal are required to build a group of figs up to this minimum number of adults? This depends in part on how many individual figs become established from a single-seed dispersal event. A bird or fruit bat, or a flock of such animals, might deposit numerous seeds of a single fig species during a single visit to an island. Dispersal of multiple-seed units is one of the possible explanations for the paradoxically high proportion of dioecious plants that have colonized tropical islands[14]. How many seed dispersal events are required to attain CPS also depends on whether rare long-distance dispersal of pollinators occurs, leading to brief recruitment episodes in fig populations below CPS.

Fig life history also affects how many independent dispersal events will be required to generate the critical minimum number of adults. CPS can be attained with a lower frequency of dispersal and establishment if fig seedlings quickly reach reproductive maturity and, perhaps more importantly, have long reproductive lifespans. Hill[40] estimates that most *Ficus* reach reproductive maturity at 10–20 years and live 100 years or more. If substantial interspecific variation exists in these traits – and this is another unexplored area of fig biology – then fig life history, as well as phenology and dispersal biology, may be a source of adaptation or preadaptation to long-distance colonization.

Colonization and establishment by fig wasps. Once the requisite number of adult fig trees is present, how good are fig wasps at colonization and establishment? Long-distance colonization by these tiny, short-lived insects would seem problematic. There is some evidence, however, showing that agaonids are capable of long-distance flights, even though most females probably enter receptive figs as close as possible to the tree from which they emerged[20, 48]. For example, two species of *Pleistodontes*, intentionally introduced onto the island of Oahu in 1921 and 1922, had by 1933 reached unaided the island of Kauai, about 100 km distant, and had established in their hosts, which had already been introduced on Kauai[5]. Ramirez[66] presents one other example that strongly suggests that fig wasps at least occasionally make flights of tens of kilometers.

How fig wasps negotiated the much longer distances required to colonize oceanic islands in the Pacific is still a matter of debate. A few species of figs, such as *F. prolixa*, *F. obliqua*, and *F. tinctoria*, range far into the coral islands of eastern Polynesia[24]. Pollinating wasps are also present[24, 68]. For van Steenis (discussion, p. 250 in Gressitt[37]) the improbability of independent successful long-distance colonization by a fig, and then later its wasp, was so great that he saw in their distribution patterns in Oceania 'formidable' evidence for some rather improbable land bridges. Most authors, however, have considered dispersal of figs and then of their pollinating wasps the most parsimonious explanation for the distribution of these widespread fig species, and three ideas have been proposed to account for what has been perceived as the least likely event in the required chain, the dispersal of fig wasps over hundreds of kilometers of ocean to a site where the host already occurs. First, Ridley[68] suggested that fig wasps may be occasionally transported safely in the guts of dispersal agents, arriving in places where figs had previously been established. Objections to this explanation are that 1) fertilized female wasps usually leave the fig before it becomes attractive to dispersal agents, and 2) only immature, unmated, wasps still inside intact ovules would seem at all likely to survive the trip, and they are unlikely to be able to mate in the defecated remains of a syconium. Second, H. G. Baker (discussion, p. 252 in Gressitt[37]) and Ramirez[66] have suggested that occasionally dispersal agents may disperse an intact fig. Objection 2) would not apply to this explanation. The third explanation answers both objections. Perhaps people carried between islands fig cuttings bearing immature syconia harboring developing fig wasps (discussion, p. 251 in Gressitt[37]). These speculations remain untested.

Discussion of the problem of how figs and wasps have colonized Oceania has largely failed to consider the following question: Is the fig species pollinated by the same wasp species throughout its range? Interestingly, in at least one case, the answer may be 'no'. *Ficus obliqua* in Fiji 'should' be pollinated by a *Pleistodontes*, but is in fact pollinated by a *Blastophaga*, leading Corner[25] to suggest that an invading *F. obliqua* may have acquired its pollinator from an indigenous Fijian *Blastophaga*-pollinated *Ficus*. Though far from conclusive, this example suggests caution in assuming that successful invasion by a fig species requires that its 'legitimate' pollinator become established.

Will fig wasps establish once they have dispersed to a new area? Even in a population above critical size, trees with receptive figs are not always available[21], so that colonists may fail to locate oviposition sites and die. If the colonists do locate receptive figs, however, the biology of fig wasps indicates that they should be relatively good at establishing populations from a very small number of initial colonists. First, a gravid female lays all her eggs in a single syconium. Second, mating takes place inside the syconium, before dispersal of the progeny. These two facts mean that the problem of finding mates in a very small population, which can lead to diminished reproduction in small populations[50], essentially does not exist. Third, we can expect fig wasps to be highly tolerant of the inbreeding that would occur in these circumstances. Fig wasps are typically extensively inbred[38, 39]; this fact, along with the constant exposure of recessive alleles to selection by the hymenopteran haplodiploid genetic system[19], will have shaped a genome tolerant of inbreeding. Inbreeding depression is the most commonly cited genetic hazard faced by small populations[50] and is thought to be an important determinant in the success of biological invasions[69, 70]. Sailer[69, 70] and Simberloff[73] believe that tolerance of inbreeding may explain why so many Hymenoptera are successful invaders.

Perhaps the most important barrier to the successful establishment of a small number of initial colonist fig wasps is the high mortality of wasps during transit from tree to tree within populations[20, 39].

Figs and fig wasps on oceanic islands. How often have long-distance range extensions of fig/wasp mutualisms occurred? The best evidence comes from the patterns of fig and wasp distribution on oceanic islands. One thing can be said with certainty: If fig biology poses barriers to long-distance colonization, these barriers have been regularly surmounted, at least by some species. Ridley[68] offers an early view: 'There is hardly any tropical island of any size but possesses one or more species of *Ficus*, and these plants, however distant from the mainland, possess their little gall-wasps in abundance.' As Corner[24] makes clear, there are some glaring exceptions to this statement: 'No native figs are reported from Juan Fernandez, the Galapagos Island, and the Hawaiian Island, or from Midway, Wake, or Easter Island'. But most Polynesian islands have at least one or two species. However, the examples most suggestive of long-distance dispersal, rather than of vicarious events that broke up a previously continuous distribution, involve only the few species mentioned above (*F. prolixa, F. obliqua*, and *F. tinctoria*) that range far into the coral islands of eastern Polynesia[24].

As stated above, the events required to explain the distribution of these species on the basis of dispersal seem improbable (though perhaps less so than competing explanations). The improbability of long-distance colonization by figs and wasps shrinks, however, when we consider the temporal scale in question. The four species of *Ficus* found on Jarak Island, 64 km W of the Malay Peninsula, by Wyatt-Smith[89], have had at least 34,000 years to get there[87]. The events leading to the distribution of *F. prolixa* from the northern Marianas to Pitcairn Island in SE Polynesia are also presumably lost in geological time.

The vast amounts of time that make long-distance dispersal plausible also make it unlikely that we can learn very much about the process from observing distributions. In one case, however, the process itself has been directly observed: the revegetation of Krakatau following its cataclysmic eruption in 1883. This example only marginally qualifies as 'long-distance' dispersal, however, since the island is midway between two large land masses (Java and Sumatra) and only 40 km from each. This is within easy striking distance for many birds and fruit bats, and probably for fig wasps as well. The information for *Ficus* was nicely summarized by Ridley[68], who noted that 3 species of *Ficus* were present by 1897, 3 more by 1906, and that by 1919 the island harbored 12 species of *Ficus*, a larger number of species than in any other genus. *Ficus fistulosa, F. fulva*, and *F. toxicaria* were abundant components of early-successional woodland on the island[13]. Their rapid spread, documented by repeated surveys, suggests extensive recruitment due to seed dispersal from the mainland, since the time involved was probably insufficient to have allowed maturation of fig trees and population growth from in situ seed production. When did the wasps arrive and establish? All that appears to be known about the wasps is that Dammerman, in a brief visit in 1921, found 3 species of fig wasps in unidentified hosts, and implied that wasps abounded in figs of every species he examined[13]. It seems likely, then, that at least 1–3, and possibly up to 12, pairs of fig and wasp species may have been present within 35 years following the eruption.

Human-aided range extensions

Many species of *Ficus* have been widely introduced as ornamentals in the tropics and subtropics of the world. Condit[22] listed a total of 108 species planted in the United States, principally in Hawaii, southern Florida, and southern California. Some 60 species may be encountered in southern Florida alone (R. Knight, pers. comm.). Comparable lists are not available for other parts of the world, but introduced figs are among the common street trees in many cities of the tropics. Adult densities of many introduced figs probably greatly exceed densities in many of their natural populations. In suburban South Miami and Coral Gables, Florida, 5 species of introduced figs occur at densities averaging greater than one adult tree per kilometer of road[54]. Approximately 500 adult *F. microcarpa* grow in Bermuda (D. Hilburn, pers. comm.); the total area of all the Bermuda islands is 53 km^2.

Thus in many cases a difficult step in long-distance range extensions by figs under natural conditions has been circumvented. Ample populations of adult trees already occur; establishment of the mutualism depends only on arrival and establishment of the wasp.

Their arrival and establishment have sometimes been brought about intentionally. But apparently unintentional introductions have also led to establishment of fig wasps in plantings of their normal hosts outside the natural range of the fig/wasp pair (table). Further cases may be confidently expected. As has been the case for other short-lived insects[69, 70], the expansion of rapid, direct commercial air flights has greatly increased the opportunity for stowaway fig wasps to arrive alive in areas thousands of kilometers outside their natural geographic range. If they land in a tropical city with numerous adults of their host fig, their chances of establishment are probably relatively high.

In the following section I summarize the history and current status of fig/wasp pairs introduced, intentionally or accidentally, and established in areas remote from

Introduced fig/pollinator pairs

Fig species	Pollinator	Area of introduction	Introduction of pollinator	Other naturalized sycophilous wasp species	References
F. altissima Blume (India to Indochina and Malaysia)	*Eupristina* sp. (*E. altissima* Balakrishnan & Abdurahian?)	Florida	Accidental	?	McKey and Kaufmann[54]
F. benghalensis L. (India)	*Eupristina masoni* Saunders	Florida	Accidental	None recorded	Stange and Knight[78]
F. macrophylla Desf. ex Pers. (Australia)	*Pleistodontes froggatti* Mayr	Hawaii	Intentional	?	Lyon[52]; Pemberton[62]; Timberlake[82]
F. microcarpa L. (widespread in tropical Asia and Australia)	*Parapristina verticillate* (Waterston)	Hawaii	Intentional	Pteromalidae: *Odontofroggatia ishii* Wiebes *Otitesella* sp. near *ako* Ishii Torymidae: *Sycophila* sp.	Condit[22]; Judd[45]; Hilburn, pers. comm.
		Florida	Accidental	Pteromalidae: *Odontofroggatia galili* Wiebes *Walkerella yoshiroi* (Ishii) *Micranisa* sp. Torymidae: *Philotrypesis emeryi*	Stange and Knight[78]; Ramirez and Montero[67]; McKey and Kaufmann[54]
		Bermuda	Accidental	Pteromalidae: *Odontofroggatia galili* Wiebes *Walkerella yoshiroi* (Ishii)	Dow and Terceira[26]; Monkman[58]; Hilburn, pers. comm.
		Mexico, Central America, Colombia	Accidental	?	Ramirez and Montero[67]
F. religiosa L. (Pakistan to Indochina)	*Platyscapa quadratriceps* Mayr	Israel	Accidental?	None recorded	Galil and Eisikowitch[32]; Galil[30]
F. rubiginosa Desf. (Australia)	*Pleistodontes imperialis* Saunders	Hawaii	Intentional	?	Pemberton[62]; Timberlake[82]; Condit[22]
		California	Accidental?	?	Ramirez and Montero[67]
		New Zealand	Accidental?	?	Gardner[33]

their natural range. I do not discuss cases like that of *F. microcarpa* in Israel, where a non-pollinating sycophilous wasp, but not the pollinator, has become established[31].

Hawaii. Aside from the frequent introductions of the pollinator of the edible fig (*Blastophaga psenes*) into subtropical and warm temperate areas in many parts of the world, intentional introduction of fig wasps seems to have been limited to the Hawaiian Islands, where figs played a large role in attempts at reforestation in the 1920's and 1930's. Hawaii has no native fig. Plans envisaged the introduction and establishment of the pollinators of numerous fig species already represented by flowering trees from previous plantings. Once seeds were available, they were to be broadcast by hand and by airplanes, in degraded forest. Introduced mynahs would aid in seed dispersal, and foresters even considered introducing additional species of frugivorous birds to help spread fig seeds[52]. The pages of the Proceedings of the Hawaiian Entomological Society offer a spotty written record of the progress of this project from 1923–1944. These brief published notices[1–12, 71, 79, 82, 83] leave us with many more questions than they answer about the introduction, establishment, and spread of fig wasps in these islands. What can be gleaned from this published record is summarized below. Judd[45] recommended the introduction of pollinators of five fig species, and in the same year *Pleistodontes froggatti*, the pollinator of *F. macrophylla*, was introduced from Australia to trees in and around Honolulu (island of Oahu)[79]. The insect was well established in Honolulu by 1923, but also at Waimea (island of Hawaii), about 250 km from Honolulu[82]. There is apparently no published record of the wasps being introduced anywhere except around Honolulu, and their sudden presence on the island of Hawaii is mysterious, though noted matter-of-factly. There is also a locality called Waimea in the northwestern part of Oahu, but Timberlake[82] states 'Waimea, Hawaii'.

In January 1922, females of a second Australian fig wasp, *Pleistodontes imperialis*, the pollinator of *F. rubiginosa*, were liberated onto a single large tree of this species on the slopes of Tantalus above Makiki Heights, a few km north of Honolulu[1, 79]. This wasp was considered well established locally by January 1923[2]. Large numbers of seeds collected from pollinated trees of both *F. macrophylla* and *F. rubiginosa* were spread over Hawaiian forests, in some cases using airplanes[83]. By 1929, both wasp species were being recorded in the remotest parts of Oahu as the plants resulting from these sowings began to reach flowering size[52]. By July 1933, both *Pleistodontes* spp. had arrived on the island of Kauai from Oahu, a distance of over 100 km, without human assistance[5]. By February 1939, both species were also recorded for the island of Lanai (ca 80 km ESE of Honolulu), without any suggestion of how they may have reached there[71].

Apparently the only other successful introduction was that of *Parapristina verticillata*, the pollinator of *F. microcarpa*. In February–May 1938, figs containing these wasps were shipped from the Philippines and Hong Kong. Several thousand female wasps emerging from these fruits were released onto trees in and around Honolulu[6, 7]. By October of the same year, the wasps were found at a site 2,000 feet higher than Honolulu and more than a mile inland[8]. By April 1939, they had reached Olaa on the island of Hawaii (once again, a leap of over 200 km goes unremarked and unexplained)[10], and in May 1939 they were first recorded from the island of Kauai. It is not known if they were introduced to Kauai or arrived there without human assistance[11].

According to Condit[22] the results of these introductions have not come up to expectations. 'Seedlings of *Ficus macrophylla* are not commonly found; those of *F. rubiginosa* are often seen growing on palms or walls. The fruits of *F. microcarpa*, however, seem to be eagerly sought by birds, and the fertile seeds are scattered far and wide. These produce seedlings which become bad weeds in undesirable places'.

The published reports on Hawaiian figs and wasps include little information on many important aspects of introductions and invasions, such as how plant material was brought to the islands so that wasps developing inside survived transport; how many wasps were released on how many trees in how many different sites; and how many adult trees were present in these areas. The most interesting conclusion that can be tentatively drawn from the Hawaiian information is that the wasps may be quite effective at moving between fig populations separated by 100 km or more. Perhaps their sheer numbers (Janzen[42] estimates that a large crop of 50,000 *F. insipida*-sized figs may release 12.5 million female fig wasps) compensate for the low probability of successful long-distance transit by any one wasp (J. Bronstein, pers. comm.).

The records note that some planned introductions of pollinators did not take place because the wasps emerged and died during transit. Were there other cases in which introductions took place but were unsuccessful? Of the successful introductions, why has one species been so much more successful than the others? Perhaps biologists working in Hawaii with access to correspondence and other records can eventually provide us with a more complete history of these interesting introductions, as well as an authoritative statement on the current status in the islands of introduced fig/wasp pairs. With further information, Hawaiian figs and fig wasps may provide case histories useful for comparisons with fig and wasp invasions that are happening now.

Florida. Three species of Asian figs are regularly producing seeds and seedlings in subtropical southern Florida, due to the introduction, apparently unintentional, of pollinating wasps. *F. microcarpa* and *F. benghalensis* are pollinated in Florida by their species-specific fig wasps, *Parapristina verticillata* and *Eupristina masoni*, respectively[78]. *Ficus altissima* is pollinated in Florida by a *Eupristina* sp. the identity of which is not yet certain[54], but which may be the species-specific pollinator of this species, *E. altissima* (J. T. Wiebes, pers. comm.).

P. verticillata is well established in southern Florida, where adults of *F. microcarpa* are abundantly planted as ornamentals. Seedlings began to appear in the early 1970's (R. Knight, pers. comm.) and many are now vigorous juveniles. Though seedlings are so far apparently restricted to suburban areas and adjacent seminatural communities, this species must be considered a potential pest in natural communities of southern Florida. Many bird species eat its fruits, including numerous migratory species that could carry seeds far from the suburban areas where adults occur[54].

How the wasps arrived is not known. The fact that four other (non-pollinating) wasp associates of *F. microcarpa* are also present in Florida[78] suggests that they and the pollinator all arrived together as larvae within *F. microcarpa* syconia. Stange and Knight[78] speculate that they were introduced inadvertently in fig-bearing material of *F. microcarpa* from Hawaii, but comparison of the fauna of non-pollinating fig wasps between Florida and Hawaii *F. microcarpa* (table) led Hilburn (pers. comm.) to question this assertion. Caution is urged in such comparisons, however. Non-pollinating fig wasp species are often patchily distributed among trees, so that a substantial sampling effort is required to determine the local fauna (J. Bronstein, pers. comm.).

How the pollinators of *F. benghalensis* and *F. altissima* reached Florida is also unknown. Seedlings of the former were first noticed in 1986 (R. Knight, pers. comm.), those of the latter species in 1987 (D. McKey, unpublished). No non-pollinating wasp associates of these species have been noted in Florida.

Seedlings of both species are so far restricted to suburban areas. These two species appear to be much less successful in producing juveniles than is *F. microcarpa*, which, as in Hawaii, has distinctly weedy tendencies and seems much more likely to invade native plant communities. Comparative studies of these three fig species and their pollinators should offer insight on the determinants of success in invasions by introduced fig/wasp pairs.

F. microcarpa in other areas. Besides Hawaii and Florida, the pollinator of *F. microcarpa* is also established in Bermuda[26, 58] (and Hilburn, pers. comm.) and in various localities from Mexico to northern South America[67]. Production of seedlings in these areas (where adult *F. microcarpa* are commonly planted as ornamentals, as in Florida) seems to have begun only about 5–10 years after *F. microcarpa* seedlings were first noted in Florida, leading Ramirez and Montero[67] to suspect Florida as the source of the colonists that effected, in ways unknown, these further range extensions of the wasp and hence of the pollinating mutualism.

In Bermuda, *F. microcarpa* were planted extensively in the late 1940's and 1950's, and about 500 adult trees now occur on the island (Hilburn, pers. comm.). Around 1980 seedlings began to appear and *P. verticillata* was found to be established. How it arrived is unknown, but the fact that two non-pollinating pteromalid fig wasps arrived at the same time (table 1) argues strongly for their having arrived together as larvae inside syconia of *F. microcarpa*. Interestingly, these two wasps are shared with Florida *F. microcarpa*, but not with those from Hawaii (table).

Juveniles of *F. microcarpa* are beginning to be a serious pest in Bermuda, and control measures are being investigated by the island's Department of Agriculture and Fisheries. The measures being considered include the first attempts ever to apply the results of research on how the pollinator population is maintained, to the problem of extirpating an unwanted introduced fig wasp. Winter is the vulnerable link in the annual cycle of figs in this marginal environment. Few trees produce crops during the winter, and Hilburn (pers. comm.) has estimated that a temporal gap sufficient to eliminate the pollinator might be produced by removing, during the winter lull, wasp-containing syconia from as few as 18–30 of the population's 500 trees. Thus far, attempts to induce trees to abort crops have been unsuccessful; another approach considered is mechanical removal by drastic pruning.

As Hilburn (pers. comm.) points out, Bermuda is an excellent laboratory for such experiments with control measures, because of the relatively small size of the *F. microcarpa* adult population, and because of the island's isolation. Further results of Bermuda's *F. microcarpa* program promise to be of great practical and theoretical interest.

Ramirez and Montero[67] document the presence of *P. verticillata* in association with planted *F. microcarpa* in a number of localities from Mexico to Colombia. The first records are from the state of Morelos, Mexico, in 1985. Based on the size of *F. microcarpa* seedlings found there, Ramirez and Montero[67] believe the wasps arrived around 1983 or shortly thereafter. The wasps have since been found in localities in four other Mexican states (Puebla, Mexico, Guerrero, and Michoacan), but *F. microcarpa* seedlings have not yet been noted in these sites. In 1986, *P. verticillata* was collected in *F. microcarpa* in San Salvador (El Salvador) and Tegucigalpa (Honduras), seedlings also being found in the latter site. According to Ramirez and Montero[67], this wasp now also occurs in Colombia. In areas where *F. microcarpa* is now producing mature fruits and viable seeds, birds and bats are dispersing them[67]. If this fig species exhibits the same weedy tendencies here as it has in Hawaii, Florida, and Bermuda, then not only these insular, marginal tropical areas, but also a large part of the neotropical mainland, might be affected by this invasive species of *Ficus*.

Other cases. Ficus religiosa, native to eastern Asia from Pakistan and India to Indochina, was introduced into Israel about 50 years ago. It is not clear how and when its pollinator, *Platyscapa quadraticeps*, arrived in Israel, but the wasp has been established there for at least 20 years and possibly much longer[30, 32]. According to Galil[30], *F. religiosa* is highly unlikely ever to exist as self-perpetuating populations in Israel. The mediterranean seasonal regime of Israel, with hot, dry summers and cool, wet winters, contrasts strongly with the monsoonal climate of the area where this species is native, and this has important consequences for the critical phase of seedling establishment. Where the tree is native, germination of seeds takes place at the beginning of the wet monsoon. In Israel the trees flower chiefly during the hottest summer months. The seeds apparently have no ability to remain dormant under dry conditions, and require continuous humidity for successful germination. The only seedlings that survive are ones that have been irrigated by nearby sprinklers, or for some other reason inhabit an exceptionally moist microhabitat[30].

Seasonality has another interesting effect on the mutualism in Israel. Galil and Eisikowitch[32] note that populations of the pollinator in Israel decrease considerably during the winter, presumably as a result of low temperatures and of infrequent flowering by the host. But we cannot guess how different this is from the pattern where *F. religiosa* is native, because in neither Israel nor east Asia has the tree's reproductive phenology been well described. If *F. religiosa* in its native area flowers infrequently during the dry monsoon – as Galil's statements[30] about germination would lead us to suspect – then its pollinator might be preadapted to infrequent flowering during the cold season in Israel.

Finally, two further cases both concern *F. rubiginosa*, one of the three fig species whose pollinator (*Pleistodontes imperialis*) is established in Hawaii. This fig has also been introduced into New Zealand, and Gardner[33] reports that its pollinator is now established there as well. According to Ramirez and Montero[67], syconia of this fig species in California develop normally and are inhabited by agaonids, probably the pollinator of this species.

What can we learn from these human-aided range extensions? These examples probably tell us more so far about the colonizing ability of fig wasps than about the colonizing ability of fig/wasp systems. In all these cases, the two most difficult steps in fig/wasp range extension have already been accomplished by human intervention: 1) a large adult population of the host fig was already present; 2) wasps were introduced, in ways yet mysterious, into areas remote from a source wasp population. All we know about fig wasps indicates that they should quite readily establish from a small number of colonists when introduced into a large population of hosts. The information presented above suggests that they have done so on several occasions.

The most interesting lessons from these incipient invasions of fig/wasp pairs are yet to come. Will they give rise to self-perpetuating populations of figs? How quickly will figs spread into natural communities? Will their spread enable us to study the process of long-distance range extension hypothesized to have occurred in nature, but never directly observed? Study of these invasions in an early phase promises to yield results of theoretical as well as practical importance.

The biology of figs in fragmented forests

'In 10–30 years, probably all tropical rain forest management will be remedial management of vulnerable remains.' (Ng[61], p. 359).

The destruction and fragmentation of tropical forests is focusing the attention of population biologists on the demographic and genetic consequences of population reduction and subdivision[50, 74–76]. The potential payoff of this research will be knowledge that will help to minimize the erosion of biological diversity in the current massive wave of species extinctions[60]. In this section I will summarize the lessons of fig biology for conservation of biological diversity in tropical forest reserves. One of the most important lessons, as in conservation biology generally[44], is that each particular fig/wasp system may differ in important ways from others. I will attempt to point to the kinds of data that will be required about each system to produce statements useful to those charged with managing natural areas in which figs are important community components.

Figs figure rather prominently in the small but growing body of literature on the role of biotic interactions in maintaining species diversity in tropical forests. In both the Old World[51] and the New[80, 81], figs have been considered keystone resources, key components of food webs whose disappearance would cause cascading extinction (but see Gautier and Michaloud[34]). If this is so, then it becomes very important to understand the requirements for persistence for fig population[5]. At the very least, we must estimate the minimum viable population sizes for keystone species and, using known densities, estimate the area required to sustain the minimum number, and design reserves accordingly[77]. Once this is done, there is still plenty of work for the reserve manager in ensuring that viable populations are maintained.

Figs as vulnerable keystone species

Leighton and Leighton[51] and Terborgh[81] have suggested that figs may often be critical species for the maintenance of biological diversity in tropical forests. Other data, reviewed here, suggest that figs, especially hemiepiphytic figs, may also be more vulnerable than many other tropical forest trees to extinction as a result of forest fragmentation, for two reasons: 1) Their minimum viable population size is large; and 2) adults often occur at low densities. Figs may thus pose difficult but crucially important problems for conservation biology.

Why are figs likely to provide keystone resources? In the phenological pattern typical of many monoecious fig species, at least a few individuals produce syconia at any time of year. A consequence is that at least a few individuals of each species bear mature fruit at any time of year. Thus even when other fruit resources are absent, some figs are available to frugivores, and tide them over the bottleneck period of scarcity. On Barro Colorado Island, Panama, for example, figs are one of very few fruit resources available during the late rainy season[29]. Windsor et al.[88] even suggest that avoidance of competition with other plant species for dispersal agents has played a role in the evolution of fruiting phenology of BCI figs.

It has been argued that if fig species were removed from tropical communities, some of these frugivores would face local extinction. Other plants dependent on those animals for seed dispersal would suffer population reductions or even local extinction, possibly dragging other species with them in their demise[51, 80, 81]. This effect may be most striking in the case of vertebrates that are highly dependent on figs, such as some birds of paradise in New Guinea[16], frugivorous bats in Panama[59], and squirrel monkeys and capuchins in Amazonia[80]. Also affected may be vertebrates that are not fig specialists but still depend heavily on them in some seasons[80]. However, where fig densities are low (see below) and large fig crops rare, animals may be less dependent on them, leading to a reduced role for these trees in vertebrate community structure[34].

Fig biology and minimum viable populations

If fig are keystone resources in tropical forests, it is important to know how to ensure their persistence in the face of population reduction and subdivision. This requires an estimate of minimum viable population size[76]. A minimum viable population (MVP) 'is not one that can simply maintain itself under average conditions, but one that is of sufficient size to endure the calamities of various perturbations'; survival 'must be measured relative to some time frame and some set of conditions' (both quotes from Shaffer[72]). Shaffer offers the following tentative definition: 'A minimum viable population for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 100 years despite the foreseeable effects of demographic, environmental and genetic stochasticity, and natural catastrophes'. MVP size is not known for any tropical tree species[41]. Its estimation requires data on population genetics and demography that rarely exist. Rules of thumb developed less than 10 years ago are considered invalid[74]. Nevertheless, understanding the implications of the data that are available on figs can get us closer than we were before to knowing how to ensure the persistence of these possible keystone species.

Four sources of uncertainty may endanger the persistence of small populations: genetic stochasticity, demographic stochasticity, environmental stochasticity, and natural catastrophes[72]. The principal genetic factor is inbreeding depression[50, 74]. Like other habitually outcrossing species[50], figs are likely to carry a substantial load of deleterious recessive alleles, and would be expected to be highly vulnerable to the effects of inbreeding. Given their phenology, figs must usually outcross, and the number of fig individuals required simply to keep the pollinator in the system may provide a buffer against strong inbreeding. Also, the mating structure of figs might provide barriers against the development of inbred local neighborhoods. Even if most of the pollen delivered to a tree during an episode of fruiting is from one or two other individuals (J. Bronstein, pers. comm.), these are not necessarily the tree's closest neighbors; mating structure is determined by proximity of individuals in time[21, 42]. Since flowering order apparently shuffles each year, 'temporal neighbors' will vary [21]. Extensive seed dispersal should add to this barrier against local spatial differentiation. In a preliminary study using relatively few loci, Valdeyron et al.[86] found virtually no spatial genetic differentiation in *F. carica* over distances of up to 500 km.

The degree of inbreeding in small populations of figs may vary, however, depending on the recruitment events that have given rise to them. If critical population size was attained by multiple founder events (e.g., dispersal of seeds from many different parents over time), the resulting population is likely to be highly outbred. If the population owes its existence to a few founder events – e.g., dispersal of multiple seeds from a single crop, or a brief episode of recruitment resulting from long-distance dispersal of pollinators into an isolated population below CPS – the population may be more inbred.

Under most circumstances, non-genetic factors may be much more important than genetic stochasticity in determining MVPs of species of *Ficus*. One likely determinant of the MVP of a species of fig is the demographic stochasticity that arises in both fig and wasp population when the number of adult figs is near the population size minimally necessary to sustain a population of the pollinator. The smaller the tree population, the greater the probability of a temporal gap between crops of two trees that is unbridgeable by the short-lived pollinator. Such a gap would lead to local extinction of the pollinator, and to that of the tree as well, if recolonization by the wasp does not occur. How likely is recolonization by the wasp? Even though the probability of successful long-distance transit by an individual of these tiny wasps is low[20, 39], the numbers of individuals involved are so great that long-distance colonization still seems to occur, at least occasionally. However, if populations of a fig species are restricted to forest fragments, then increasing fragmentation should reduce the frequency of such colonization events, for two reasons: 1) the distances that must be traveled between fragments are greater; 2) the number of trees releasing potential colonizing wasps decreases as forest area decreases.

Thus, superimposed upon the demographic hazards faced by all outbreeding trees in species-rich tropical forest[41], fig populations undergoing reduction and subdivision are faced with the additional problem of maintaining a short-lived, species-specific pollinator. Furthermore, figs often occur at densities that are low even when compared to those of other tropical trees (see below). If MVPs of figs are large, and many fig species are rare, then large minimum areas will be required if figs are to persist. For one of the 700-odd species of *Ficus*, data exist that enable an estimate of CPS, and from this a very conservative estimate of MVP. For other fig species, data are available on density of reproductive adults. For not a single species of fig do we have all the pieces of the puzzle to calculate its minimum area requirement.

F. natalensis – estimating CPS and MVP

The simulation model of Bronstein et al.[21] discussed above was developed to examine the process of pollinator establishment in isolated fig populations, but can equally well be applied to analyze vulnerability of populations reduced by habitat destruction and fragmentation. Recall that for *Ficus natalensis* median CPS required to sustain the pollinator population for four years was 95 adult trees, and that in 100 runs of the model, CPS ranged up to 294 trees.

How can these results be applied to the problem of ensuring persistence of fig/wasp mutualisms in fragmented forest? First, from the perspective of conservation biology, the time frame must be expanded. The four-year period that they considered, though an appropriate time frame for examining colonization (and approaching the limits of affordability in use of computer time!), is very short when we are concerned with minimizing species extinctions. As a rough first approximation, we can treat 100 runs of four years as an adequate sample of temporal variability and extrapolate to longer periods. If the probability that 95 *F. natalensis* trees can maintain a pollinator population for four years is 0.5, then the probability that they can maintain it for 20 years – assuming no colonization events – is 0.5^5, or only 0.03. If 294 trees can maintain a pollinator population for four years with a probability of 0.99, the probability they can maintain it for 1000 years is 0.99^{250}, or about 0.08. If Shaffer's[72] tentative criteria for MVP of a 99% chance of remaining extant for 1000 years are to be met, population size must be substantially higher than this.

For the moment, however, let us consider acceptable a 1% probability of wasp extinction in the short term, and estimate CPS for *F. natalensis* very conservatively at 300 adult trees, plus the juveniles necessary to maintain this number of adults indefinitely. Let us make the further assumption – which will be examined in a later section – that sustaining the pollinator is the crucial factor determining MVP.

Estimating minimum area

We may next ask what area of forest must be preserved to ensure maintenance of MVP. This question has two parts. First, how dense are fig populations? Second, will fig species persist at these densities when forests are fragmented? The first part of the question is conceptually straightforward, the second part is not. Neither can be satisfactorily answered at present.

Fig densities in natural communities. Fig populations are often dense in open communities such as neotropical palm savannas[64, 85] and in secondary succession[23]. Scattered information on their densities in mature tropical forests, however, indicates something very different. Although the family Moraceae and the genus *Ficus* are abundant taxa in forests of all three major tropical regions[35], the genus is typically represented by numerous sympatric species, each rare. This pattern has been documented in Asia[51], Africa[34, 56], and the neotropics[36, 41, 80, 84]. Like other Moraceae[35], *Ficus* spp. seem to be even rarer in sites characterized by relatively poor soil (A. Gentry, pers. comm.).

In a 50-ha plot in old-growth forest on Barro Colorado Island, Panama, Hubbell and Foster[41] found 8 species of figs, all of them relatively rare. Only one species occurred at densities greater than 1/ha (1.3/ha); densities of the other seven ranged from 0.12/ha to 0.3/ha. Todzia[84], also working in old-growth forest on Barro Colorado Island, recorded 12 species of hemiepiphytic *Ficus*, occurring at a total density of 3.0 individuals/ha, equally divided between large free-standing individuals and smaller wholly epiphytic individuals. At Cocha Cashu in Manu National Park[80], a number of fig species occur, but the density of most is only 1–5 individuals/km^2. In a 1-ha tree plot in Manu, Gentry[36] recorded 7 species of *Ficus*, represented by 11 individuals large enough to have reached the ground. Fig densities are similar in the Rio Palenque site in Ecuador, and figs do not seem to be any more abundant in any other species-rich wet forest in the neotropics (A. Gentry, pers. comm.).

Data exist for two African forest sites. At Makokou in Gabon, *F. ottoniifolia* occurs at densities of less than 1 tree/10 ha[55]. Most of the 26 other species of *Ficus* in this site[28] are similarly rare, except in riparian situations, ranging up to 0.32 individuals/ha, and with a mean overall density of 1.5 individuals/ha for 20 hemiepiphytic species grouped[34]. In riparian forest, overall fig density was 46.5 individuals/ha[34]. In the Tai Forest of Ivory Coast, Michaloud and Michaloud-Pelletier[56] censused 20.91 ha, recording 19 species and 98 individuals of *Ficus* whose roots reached the soil. Total density of figs was 4.7 individuals/ha. All 19 species occurred at densities of less than 1/ha, and 3 species were represented by a single individual.

Finally, in Asia, Leighton and Leighton[51], working in primary forest in Kutai National Park, East Kalimantan (Borneo), Indonesia, recorded a total density of figs averaging 3.3 adult figs/0.5 ha, divided among 30 species. This works out to a mean density of about 1 individual/5 ha. In a Malaysian study, Poore[63] enumerated upper canopy trees only, finding two species of *Ficus*, each represented by a single individual in 23 ha.

Thus in the species-abundance curves of many tropical forests, *Ficus* spp. consistently form part of the long tail of rare species that pose difficult problems for tropical forest conservation[41, 61].

There are several problems with attempting to use data such as these in estimates of the minimum area required to support a viable population. First, enumerations of hemiepiphytic figs usually distinguish between wholly epiphytic individuals and those whose roots have reached the soil, and commonly deal with only the latter category. This category may not correspond to the category of reproductive adults. Secondly, extrapolating the densities recorded in these samples to larger areas in the same site is a questionable procedure. If the habitat is heterogeneous and the distribution of a species is patchy, a sample of a small area may overestimate or underestimate global abundance. The rarer a species, the greater the area is that must be sampled to find patchiness and to identify its causes[41]. Some figs are known to be habitat specialists. *F. natalensis*, for example, is strictly riparian. Figs of the subgenus Pharmacosycea, at least in the neotropical region, may be habitat specialists on alluvial soils (A. Gentry, pers. comm.).

Will these densities remain unreduced in fragmented forests? Both area effects and edge effects[75] may act to decrease fig density in small populations. If these effects are large enough, populations that are above CPS may be gradually reduced to a point where maintenance of the pollinator becomes uncertain.

Area effects are causes of population reduction attributable to size of a reserve or other habitat fragment. If a forest fragment is not large enough to support an intact coterie of fig dispersal agents, for example, fig density may decline as fewer seedlings establish. Pollination success may also be limited by area effects. Reduction of a population below CPS is of course itself an example of an area effect. But even if a reserve harbors a fig population just large enough to maintain a local pollinator population, trees should more often fail to reproduce than in populations well above CPS[21]. Lower seed set by individual trees and/or lower frequency of seedling establishment, due to inadequate seed dispersal, should lead to fewer seedlings and hence to lower adult density, though the magnitude of this reduction and the rate at which it will take place depend on stage-dependent survivorship in figs, about which little is known.

Edge effects – negative effects on populations within a habitat fragment due to influences from outside – are also conceivable. Depending on behavior of seed dispersers, a large proportion of seeds may be lost through dispersal into unsuitable habitat outside forest fragments. In fragmented forest, this outflow may not be matched by inflow. If many seeds are dispersed over relatively long distances, then this type of edge effect may extend even deep into large forest fragments[43, 44]. On the other hand, forest fragmentation may alter the shape of the 'seed shadow' – the spatial distribution of a tree's seeds following dispersal – in such a way that edge effects are minimal. If monkeys that are restricted to mature forest, for example, are important dispersal agents for a species of fig, the seed shadow may be truncated, since these animals remain in the forest fragment, and the density of dispersed seeds may increase within the fragment. Birds or bats, in contrast, may carry fig seeds from one forest fragment to another, with few seeds dropped into unsuitable habitat between fragments.

While the direction and magnitude of effects of forest fragmentation on fig density will surely vary from case to case, the lesson from these considerations is clear: a forest fragment that contains more than the critical population size of adults will not necessarily generate enough surviving juveniles to maintain this density over the long term. Minimum viable populations of figs may be substantially larger than the critical population size required to maintain a population of the pollinator.

Figs in areas between fragments of mature forest. So far I have tacitly assumed that the areas between fragments of 'undisturbed' tropical forest make a negligible contribution to maintaining populations of fig species and of animals that depend on them. The extent to which this assumption is justified depends in part on the effect of disturbance of fig densities. Some types of disturbance result in great reduction of fig densities. Density of hemiepiphytic figs in East Kalimantan, for example, is drastically reduced by logging, since the large timber trees that are removed often act as their hosts[51]. Logging has a similar effect on fig density at Kuala Lompat in Malaysia[49]. To cite a more extreme example, replacement of tropical forest by row agriculture, plantations, or pasture, may virtually eliminate figs between forest fragments.

However, areas between fragments of 'undisturbed' forest cannot always be considered a sea of habitat unsuitable for figs. Many fig species thrive in early successional forests[23, 34, 42, 56, 57], and if the disturbance regime allows forest regeneration, fig density overall may often be higher in areas between fragments of mature forest than within them. However, the species abundant in second-growth are a different set, often terrestrial rather than hemiepiphytic[34, 57]. There are likely to be at least some mature-forest fig species that disappear in disturbed areas. In other circumstances, though, a fig population may include individuals in both disturbed areas and fragments of undisturbed forest. Sometimes figs are left standing as shade trees when the forest is cut[42]. Fig species present in mature forest may become abundant in secondary forest, cleared pastures, and logged areas (e.g., *F. pertusa*; J. Bronstein, pers. comm.), or may be planted, e.g., as fencepost lines throughout northwestern Costa Rica (W. Ramirez, pers. comm.). If the pollinators of these species visit trees in such open sites, reserves of mature forest will not be necessary to conserve these species.

For many of the species of animals dependent on figs, however, the situation may be very different. Some frugivorous animals may use figs in both undisturbed and disturbed forest, but the focal species of conservation efforts are vulnerable usually because they are restricted to fragments of mature forest. For these species, it is only fig density within fragments of undisturbed forest that matters.

Local extinction and global extinction. If populations of figs and their wasps suffer local extinctions, when will these begin to add up to global extinctions? Here we find a relative bright spot in the implications of fig biology for conservation of biological diversity. Ng[61] notes that in Malaysia, species of *Ficus* are usually wide-ranging, with low rates of endemism relative to many other large plant taxa. Thus a network of large reserves in a variety of habitats has a good chance of preserving most of the regional *Ficus* flora.

Low rates of endemism may also be typical of *Ficus* elsewhere on continental landmasses. Of the 60 species of figs recorded for Cameroon[18], only one – *F. oresbia*, known only from the type locality – is restricted to this country, with one other species known only from submontane forests in Cameroon and three continental islands in the Gulf of Guinea. Only two species are restricted to the forests of Cameroon and Gabon, an area of high endemism in many plant taxa. Fully 39 of the 60 species occur in all three of the major African forest blocks, are widespread in the continent's extensive savannas, or occur throughout most of subsaharan Africa.

On the other hand, the fig flora of ancient continental islands such as Madagascar[17] or New Caledonia[24] is characterized by the same high rate of endemism as other components of their biota.

Two perspectives on figs in conservation biology

One half of this paper has considered figs as vulnerable rarities, the other half as biological invaders. How can these two views be reconciled? In part, this seeming paradox is a result of artificial situations created by human intervention. A crucial variable in the functioning of fig/wasp systems is fig population size. If we create large fig populations in new areas by planting figs abundantly as ornamentals, we make them much better invaders than they are in nature, by circumventing the major difficulty in long-distance colonization by fig/wasp systems. Similarly, if we decrease the size of fig populations by reducing their habitat to isolated fragments, we can render fig and wasp populations vulnerable to extinction.

These two perspectives may also reflect the different environmental contexts faced by native and introduced plants. Figs, like many other plants, may exhibit ecological release when introduced into areas largely free of natural enemies. One kind of fig may be a rarity or a weed, depending on the context. I am reminded of an anecdote overheard at a symposium on exotic pest plants. According to this story, Australian entomologists are considering investing in a search for insect herbivores of a plant, native to Florida, that is invading *Melaleuca* forests in Australia. Ironically, this plant is among those Florida natives suffering from the relentless advance of introduced Australian *Melaleuca*. The biology of introduced figs suggests the interest of comparative studies of fig herbivores and pathogens.

The difference in perspectives may also be due to the great biological diversity represented in this plant genus. Invading species are often those that depend on disturbed, invasible habitats. Fig species certainly vary in their response to disturbances, and some are probably better preadapted to be invaders than others. In many areas today, some fig species may be dramatically increasing while others are simultaneously declining, as mature forest disappears and more area is occupied by logged forest, pastures, and secondary succession. An important component of this varied response to disturbance is doubtless the great diversity in growth strategies of figs, which include free-standing trees, vines, epiphytes, hemiepiphytes, and full-fledged stranglers. Understanding the consequences of this diversity will be a further important step in the comparative biology of figs.

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