

Ecological and evolutionary dynamics of fig communities

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Summary. I review the status of five topics in fig research: pollen-vector versus seed production, flowering phenology and wasp population dynamics, monoecy versus dioecy, parasite pressure, and fig wasp behavior. I raise several new questions based on recent research on two components of fig reproduction: pollen-donation (male) and seed-production (female) success. I focus on how these two components of reproductive success depend on the flowering phenology of the figs and the population dynamics of the pollinator wasps.

Key words. Coevolution; comparative method; development; *Ficus*; fig; Hymenoptera; mutualism; parasite; phenology; phylogeny; pollination.

Introduction

In 1979 three important papers on fig research were published. Wiebes³⁹ surveyed work on phylogenetic reconstruction of figs and their pollinating wasps, with an emphasis on coevolutionary history as revealed by phylogeny. Hamilton¹⁶ noted that the unusual life cycles of pollinator and parasite fig wasps have caused three convergent characters to evolve repeatedly and independently: wingless males, lethal combat among males, and male dimorphism in which some males are winged and others are wingless. Janzen²³ provided an overview of many ecological and evolutionary questions regarding the wasp-fig symbiosis, including aspects of flowering phenology, relative seed and wasp production per fig, and wasp movement.

When these three papers were written, there were just enough data available to sketch out important questions for future study. Some progress has been made recently on a few questions and, of course, many new questions have been raised. In this paper I will briefly summarize new observations and the current status of five topics in fig research. I will rely on the 1979 papers for biological background and detailed reference lists on past work.

Wasp versus seed production

A monoecious fig inflorescence (syconium) contains hundreds of pistillate and fewer staminate flowers. Each pistillate flower eventually produces one seed, one wasp, or nothing. Pollen is dispersed only by female pollinator wasps, so the number of female wasps produced indicates the plant's success through male reproductive function. The number of seeds per syconium indicates success through female function.

Bronstein^{4,5} studied naturally occurring spatial and temporal variation in the numbers of wasps, seeds and empty ovaries per syconium in *Ficus pertusa* in Costa Rica. Syconia that were entered by female pollinator wasps (foundresses) early during their period of receptivity tended to have many foundresses, to be small, and to produce a high proportion of wasps relative to seeds. By

contrast, syconia entered later tended to have few foundresses, to be large, and to have a high fraction of seeds relative to wasps. Because of within-crown synchrony of syconium maturation and of wasp arrival, individual crops tended to produce syconia that varied little in size and in relative wasp versus seed production, whereas there was much variation among crops. Single crops therefore tended to be relatively more successful as pollen donors when entered early and as seed producers when entered late. Total success per syconium, seeds plus female wasps, was considerably lower for crops entered relatively early during the period of receptivity.

These general trends in wasp versus seed production occurred both spatially, among different trees, and temporally, among different crops on the same tree. By collecting both spatial and temporal data, Bronstein was able to conjecture that the observed patterns are caused by developmental variation common to all individuals rather than by genetic variation among individuals^{4,5}.

This hypothesis about the developmental basis of ecological correlations was tested more stringently by experiment. Bronstein⁴ bagged different branches of the same tree and introduced wasps at different stages of syconium receptivity. Variation among experimental branches within trees was as great as variation among crops entered at different stages, suggesting that most observed variation was caused by an interaction between developmental processes and variation in wasp abundance.

Herre²⁰ compared numbers of flowers, foundresses, wasps, and seeds per syconium among 12 species of monoecious figs (subgenus *Urostigma*) in Panama. He suggested that these fig species can be ordered along a continuum, from those with a small number of flowers, which produce relatively low proportions of viable seeds and high proportions of female wasps, to those with a large number of flowers, which produce relatively high proportions of viable seeds and low proportions of female wasps. These observations imply an evolutionary and perhaps adaptive trend among this suite of characters.

An independently derived estimate of phylogeny might suggest possible explanations for the observed covariation among these characters. For example, there may be

a continual trend toward larger or smaller flower number throughout the complex of *Urostigma* occurring in this area, suggesting a strong directional selection pressure on flower number or some correlated character. By contrast, if flower number is independent of phylogeny, then each species may be adapted to, for example, its own environmental conditions and mode of dispersal.

Comparisons within species across their geographic range would be an interesting supplement to Herre's data. Several *Urostigma* species are, according to current taxonomy, distributed through the Caribbean islands to Panama and from Mexico southward through Central America^{1,2}. One could use geographic distance as an indication of the phylogenetic distance among populations within species, or if possible, resolve the phylogeny of populations within species by morphological and biochemical characters. If, for example, fig size and related characters of a single species increased steadily across its range, in a manner typical of clines, or according to some a priori prediction concerning development or adaptation, then one may hypothesize particular processes to guide further experimental and comparative studies. At the end of this section I propose one plausible adaptive explanation for variation in syconium size among species.

There is an interesting contrast between Herre's²⁰ among-species and Bronstein's⁶ within-species data: among species, smaller compared with larger syconia tend to have fewer flowers and fewer foundresses, whereas within *Ficus pertusa*, smaller compared with larger syconia have similar numbers of flowers but more foundresses. These contrasting patterns may be framed within a developmental context. In particular, syconium development and receptivity to foundresses can be described by three timing mechanisms: 1) the period during which flower primordia multiply and flower number is determined; 2) the onset and subsequent period of receptivity to foundresses relative to the developmental stage of other syconium characters, including overall size (see above); and 3) the amount of time between the first entry by a pollinator and the sealing of the ostiole.

The developmental causes for among- and within-species trends can be explained in terms of these three timing characters of syconia. a) Among-species variation. The species-specific range of flower number is determined early in development by mechanism (1). The temporal window of foundress receptivity relative to the developmental stage of other syconium characters sets the range of syconium size for a fixed number of flowers (2). b) Within-species variation. High wasp density will lead to foundresses entering early during the window of foundress receptivity (2) and to many foundresses arriving at each syconium during the fixed entry period after the first arrival (3). This yields a negative correlation between syconium size and wasp density during receptivity. This within-species prediction remains to be tested on Herre's species.

Herre observed that, among species, syconia with fewer flowers have relatively fewer foundresses. This may depend on differences in wasp density among species, with smaller syconia associated across species with low wasp density. Herre suggests that circumstantial evidence is against this explanation²⁰. An alternative and testable developmental explanation is that species with a relatively short period of flower multiplication, leading to fewer flowers, also have relatively shorter periods for foundress entry after the first arrival (3), leading to fewer foundresses per fig.

Another pattern likely to occur is variation in syconium size among species that have a similar number of flowers. In this case the period of foundress receptivity may be shifted later in those species with larger syconia (2), since syconia appear to increase in size when foundresses enter relatively late in development^{4,5}.

Studies of syconium development, such as those pioneered by Verkerke³⁷, will be important for determining the role of the three timing characters in both ecological variation within species and evolutionary divergence among species.

The tree developmental processes suggest how variation is formed. The striking range Herre²⁰ observed in syconium size (dry wt: 0.05–2.6 g) and flower number (180–2051) among twelve species in one location suggests that potent selective forces act on variation in syconium characters. I suggest that competition for seed dispersers leads to adaptive character displacement in syconium size, with each size category of fruit favored by different dispersers.

Grant^{13,14} has reviewed the problems of testing character-displacement hypotheses. One simple approach would be to partition variation among species in fruit size and other syconium characters into variation within locations and among locations. If variation within locations is greater than expected by chance, then divergent selection pressure on syconium characters is implicated. Many alternative explanations would of course remain, and these would have to be sorted out by analyzing phylogenetic and biogeographic history.

Population dynamics of figs and pollinating wasps

In the previous section I described how pollinator wasp density affects the ratio of wasp to seed production per syconium. What determines wasp density? The interdependence between wasp and fig life cycles makes this question particularly interesting. Pollinator wasp species are, in general, restricted to a single fig species, and figs usually have only one pollinator species³⁹. When wasps emerge from a syconium they must find a receptive syconium to enter within a few days or else perish. A short gap in the population-wide flowering of a fig will therefore cause local extinction of its pollinator wasp. In general, the spatial and temporal pattern of flowering

(phenology) of the figs determines wasp population dynamics.

Several questions arise concerning wasp population dynamics and fig flowering phenology. How can a pollinator wasp population be maintained if a constant source of receptive syconia are needed? What are the dynamical properties of wasp population size? What are the sources of phenological variation within fig populations? What causes phenological variation among species?

In this section I consider only monoecious figs, since very little data are available for comparison among dioecious species. For a discussion of phenology in a dioecious species, see Kjellberg et al.²⁶

I begin by considering the sources of phenological variation within populations and the effects of this variation on wasp population dynamics. Population phenology can be described by the number and spatial location of syconia at a particular developmental stage for each day of the year. Population-wide pattern can be partitioned into two levels. First, the temporal correlation among syconia within an individual crown describes the amount of individual synchrony or asynchrony. Second, the temporal correlation among individuals describes seasonal flowering variation and the degree of population-level asynchrony among individuals.

Fig phenology is often described as synchronous within each crown of an individual and asynchronous among individuals. This trend is often observed, but is not a general rule and is, at present, poorly quantified. Janzen²³ and Bronstein⁶ discussed asynchrony within crowns, and Milton et al.³⁰ and Windsor⁴⁰ described tendencies toward population-wide flowering peaks in several Panamanian species.

Within-crown asynchrony can have profound effects on pollinator population dynamics and patterns of pollination because it can allow wasps simply to move from one part of a tree to another²³. A single tree would thereby maintain a private population of pollinators, avoiding pollen limitation and generally suffering the usual costs and enjoying the usual benefits of inbreeding. The problem for figs is more interesting, however, because a tree that manages to maintain wasps during a period of sparse flowering can be a very successful pollen donor when other plants enter a flowering peak.

Janzen²³ pointed out that only a few asynchronous syconia within a crown can have a significant effect on pollen flow and wasp population dynamics. For example, if each tree were absolutely synchronous within its crown, then many trees flowering asynchronously would be needed to guarantee a constant source of receptive syconia in a local population. By contrast, if some trees had a few asynchronous syconia timed in a way that wasps could emerge from and reenter syconia within crowns, then far fewer trees would be needed to maintain a pollinator wasp population. Following this logic, Janzen²³ hypothesized that marginal populations with low densi-

ties would be more likely to have within-crown asynchrony than populations or species at high density.

Bronstein⁶, reviewing more recent data, concluded that although within-crown asynchrony does occur in some marginal populations, it also occurs in areas that are likely to have high plant densities. She proposed a modified version of Janzen's explanation: within-crown asynchrony may reduce the number of individual plants required to prevent a temporal flowering gap and pollinator wasp extinction. Bronstein's explanation does not require within-crown wasp transfers, which depend on a very particular timing of wasp receptivity and emergence. I propose an alternative explanation for within-crown asynchrony. Individual plants may be resource-limited when all syconia of a synchronous crop get pollinated, whereas a plant may be pollen-limited when pollinator density is low. Selection favors asynchrony because it reduces the probability of either extreme. Within species, a developmental process that caused increasing within-crown asynchrony with increasing resource stress would be consistent with this adaptive scenario. Among species, consistently high or low pollinator density would be equally likely to favor asynchrony.

Turning now to the timing of flowering among plants, the population-wide flowering peaks observed in some species^{30,40} seem fairly easy to explain. Seed dispersers, water, light and nutrients typically have annual cycles which probably favor flowering and fruiting cycles. A more difficult question is why some plants would flower when conditions are poorer than during these seasonal peaks. Certainly there will be fewer plants competing for available pollinator wasps during off-peak periods, although there will also be fewer wasps except during the period following the flowering peak. Likewise, there will be fewer plants competing to donate pollen, but also fewer receptive plants except as the population moves toward its flowering peak. Parasite pressure is also likely to diminish during the off-season (see later section on 'Parasitoids, seed predators and inquilines').

One hypothesis is that annual flowering patterns are influenced by frequency-dependent competition for obtaining pollinating wasps and for donating pollen²⁷. The frequency-dependent hypothesis makes a specific prediction: the combined seed dispersal and pollen donation success of each plant, matched for size and resource availability, will on average be equal throughout the year. If this were not so, then selection would favor modification of plants that were performing worse than average. The equality of success is, at least in principle, a testable hypothesis. This hypothesis can be called 'adaptive,' since it assumes that phenotypes have been molded primarily by factors that affect reproductive success, such as parasites and density-dependent competition for pollen and seed dispersers.

A developmental scenario could also explain population-wide flowering patterns among individuals. Suppose that plants flower whenever they have acquired enough re-

sources. If the environment is seasonal, then plants would tend to acquire resources seasonally and flower in a partly synchronous manner. In an aseasonal environment plants would flower asynchronously.

Developmental mechanisms can be inferred by ecological and experimental studies within species. For example, repeated sampling of single individuals can establish whether resource level, size, or other ontogenetic properties affect flowering, and whether individuals have a seasonal rhythm. Windsor's⁴⁰ study of Panamanian species did show a tendency for larger individuals to flower more frequently (see also Milton³⁰). Michaloud²⁹ studied the phenology of half-sibs of *Ficus natalensis* planted in a common garden. He found no effect of genotype on flowering pattern, and no seasonal rhythm within individuals.

The developmental and adaptive hypotheses are not necessarily alternative explanations for asynchrony among individuals. For example, the proposed pattern of development may be an adaptively evolved proximate mechanism that determines how equality of reproductive success is achieved. On the other hand, closely related species may share the same developmental pattern, which constrains some of these species from evolving developmental patterns that would otherwise be favored by selection.

Monoecy versus dioecy

In the previous two sections I discussed wasp versus seed production and flowering phenology in monoecious fig species. These two factors interact to determine an individual plant's male and female components of reproductive success. Within monoecious populations particular crops will sometimes be relatively more successful as a male (pollen donation) and sometimes relatively more successful as a female (seed dispersal)^{4, 5}. Whether different individuals specialize in male versus female function is unknown.

In dioecious species separate individuals specialize in making either only seeds or only wasps, and the two types are morphologically distinct. Although roughly one-half of all fig species are dioecious, dioecy has apparently evolved from monoecious ancestors only twice² (but see Ramirez³⁴). Phylogenetic comparisons and biogeography therefore provide only limited information about the origin of functional dioecy.

The difficulty of studying the origins of dioecy is similar to the problem of inferring factors that promoted the origin of eusociality in insects: existing species have obviously been modified since the time of evolutionary transition, and only a small number of transitions actually occurred. Insect species that currently exhibit some primitive social traits have been useful for comparing hypotheses about origins. In particular, closely related lineages that vary in degree of sociality, or individual

species in which sociality varies with ecological conditions, suggest which factors favor eusociality.

This approach to studying the origins of eusociality suggests that the origins of dioecy can be analyzed by measuring variation in wasp versus seed production in monoecious species²⁰ (see above section on 'Wasp versus seed production'). Within monoecious species, certain traits may favor relatively greater wasp production and pollen donation compared with seed production and dispersal. For example, producing more and perhaps smaller syconia per crop, flowering more frequently, and not using resources to ripen fruits and attract dispersers may yield higher pollen donation success and lower seed dispersal than producing fewer and perhaps larger syconia that are more attractive to dispersers. Measuring the amount of dimorphism within populations for these two strategies and the successes of each will indicate the tendency toward dioecy within monoecious species. Comparing the amount of dimorphism among species may also suggest hypotheses about the ecological factors that favor the origins of dioecy.

Dioecious figs appear to cope with seasonal environments better than monoecious species (review in Bronstein⁶). This observation provides very little information about the origins of dioecy, and whether dioecy is an adaptation for seasonality. A much more interesting and tractable problem is the patterns of biogeographic radiation found in monoecious and dioecious figs and the adaptive trends found within each group. For example, one could compare trends in phenology and seed dispersal syndromes within monoecious and dioecious lineages with similar biogeographic histories. Evolutionary patterns in radiations into increasingly seasonal environments might suggest how monoecious and dioecious figs respond differently to seasonality.

A clue about the role of seasonality in the origins of dioecy may be obtained from monoecious species. Consider a monoecious species with a population-wide flowering peak. Plants that flower between peaks can contribute heavily as pollen donors if they release many wasps in the peak period of flowering. In particular, plants flowering between peaks may maintain wasp populations while expending a small amount of resource by flowering asynchronously within and among individuals, with small crop sizes and little investment in attracting seed dispersers. As the population enters its flowering peak, the plants that flowered in the off-season may produce a larger crop and release many pollen-carrying wasps.

This pattern, in which pollinators are maintained at low density in the off-season and then built up before the seed-dispersing trees flower, is similar to Kjellberg et al.'s²⁶ description of the phenology of male trees (caprifigs) in the dioecious edible fig *Ficus carica*. *F. citrifolia* in Florida may be a good monoecious species on which to test this scenario, since it appears to have a distinct flowering peak in May-July (pers. obs.).

Parasitoids, seed predators and inquilines

Each fig species maintains a large community of inquiline arthropods, including nematodes, mites, dipterans, and several families of chalcidoid wasps^{3, 23, 28, 35, 38}. Little is known of these inquilines concerning their natural history, ecological dynamics of populations, or evolutionary affinities. Some wasp species are probably seed predators, reducing the female component of fig reproductive success. Others are parasitoids of the pollinator wasps, reducing male reproductive success. Finally, some are probably commensals and have little effect on reproductive output¹¹.

Data on distribution and abundance of inquilines are too sparse at present to draw any empirical conclusions. Anecdotes suggest that wasp inquilines may, at particular times and locations, be more abundant in syconia than pollinator wasps, whereas at other times and locations the inquiline wasps may be rare⁴.

These inquilines have a potentially large effect on total reproductive success, and different inquiline species very likely have a differential effect on male and female components of success¹². I suggest that these inquilines may be a potent selective pressure shaping fig phenology.

If costly inquiline loads are reduced for individuals that flower away from a population-wide peak, then these reproductive advantages may partly explain why some individuals do flower at times when resources such as light, water, and seed dispersers are relatively low. One cost of flowering at off-peak times may be a reduction in available pollinator wasps. This comparison between the benefits of reduction in inquiline load and the costs of reduction in available pollinators raises an interesting question. Do population sizes of pollinators and inquilines respond differently to the changing availability of receptive syconia?

If inquilines were more sensitive than pollinators to low syconium abundance, then one would expect lower densities of inquilines in the off-season and a consequent reproductive advantage for flowering during the off-season. I expect that hymenopteran inquilines are indeed more sensitive, since a female lays only a few eggs in each syconium by ovipositing through the outside wall, whereas a pollinator wasp lays many eggs in each syconium. The oviposition pattern of inquiline wasps suggests that specialists on a single species will be more sensitive to population crashes of figs than generalists. Within-crown asynchrony is another interesting dimension affecting the population dynamics of pollinators relative to inquilines. Synchronous crowns probably allow inquilines more easily to find syconia at the proper stage for oviposition because they often use more than one syconium, whereas pollinators use only one.

Inquilines may also play a role in shaping sexual dimorphism and a tendency toward dioecy. Some inquiline species probably specialize as seed predators and affect only female success, whereas others specialize as pollina-

tor parasitoids or kill pollinators while competing for seed tissue and affect only male success. Morphological and phenological traits that help to avoid one or the other of these inquiline types may favor sexual dimorphism in the figs.

The type of ostiole and wall thickness of syconia may also be shaped by seed predators and parasitoids. For example, selection may favor divergence of these characters among species that have overlapping ranges, thereby minimizing the success of generalist inquilines. If this were the case, then these characters would vary more within a locality than predicted by a null model based on phylogeny and estimates of ancestral character state. Along these lines, dioecious species may originally have been very good at escaping the abundant inquilines of monoecious species. For example, a dioecious species with a seasonal flowering cycle may not produce any seeds over several months, which would prevent seed predators from easily radiating from monoecious species. This idea is difficult to test, but evolutionary patterns of parasite radiation onto dioecious species and the current overlap of parasites between co-occurring monoecious and dioecious species may be informative. Obviously, work on inquiline biology and phylogeny is needed^{35, 38}.

Wasp behavior

In the previous sections I have focused on factors that influence the reproductive success of figs, including pollinator and inquiline population dynamics. These fig associates' reproductive biology, morphology and population dynamics are in turn influenced by many fig traits. To obtain a full understanding of fig biology and the fig community we must understand the ecology and evolution of these associates. On the whole, very little information is available. Here I will briefly mention some interesting areas of research that have emerged from preliminary studies.

Complex morphology and behavior are often associated with pollen transport. The particular morphological structures and motor patterns vary widely^{32, 33}. At present only a few complete descriptions of behavior and morphology have been published (reviewed by Frank⁸). Mechanisms of pollen transport may influence the number of pollinators required to pollinate a given number of flowers in a single syconium. As discussed above, the number of pollinators per syconium varies widely among species, may vary temporally and spatially within populations, and may influence and be influenced by developmental characters of the syconium.

Oviposition behavior is another important trait. For example, style width may be more important than length in determining if a wasp can successfully reach the ovary and lay an egg³⁶. If true, this fact bears on the evolution of ovipositor length, flower number, style-length polymorphism, and patterns of wasp versus seed production. Descriptions of oviposition and pollination are also

needed to understand the diversity of developmental processes of the syconium that Verkerke³⁷ has recently described.

The behavioral mechanisms by which pollinator wasps find host plants and choose to enter a particular syconium influence the distribution and abundance of pollinators. Once again, few data are available. If one watches pollinator wasps on a receptive tree, it appears that choice is being exercised over which syconium to enter. Janzen²⁴ suggested that wasps avoid syconia that have already been entered. Frank⁷ found by experiment that this is true, but the mechanism is better described by the closing of the ostiole after the first wasp has entered – that is, the tree prevents the wasps' entry. Pollinators of *Ficus citrifolia* in Florida did not discriminate between syconia that were recently entered and those that had never been entered, but avoided and appeared to have difficulty penetrating into syconia that had been entered a day earlier. Other aspects of pollinator choice include discrimination among fig species^{4,7} and discrimination between syconia in which inquiline wasps have or have not oviposited⁷.

Sex ratio of the pollinator wasps also influences their population dynamics, since population growth depends on the number of females. Pollinator sex ratios have received much attention recently. Hamilton¹⁶ and Herre¹⁸ made comparisons within populations and showed that foundress number is positively correlated with the frequency of males produced in a syconium. Kjellberg²⁵ and Frank⁹ found similar results based on experimental manipulation of foundress number. Herre¹⁹ found, by comparison among species, that variation in foundress number predicted the degree of developmental plasticity in sex ratio within species.

Sex ratio biases depend on patterns of male competition for access to mates¹⁵. The wingless pollinator males search for mates in the confined cavity of the syconium during a limited period of time. In many fig species, one or more males chew an exit tunnel through the wall of the syconium, which causes the mated females to leave the syconium. This situation favors a group of brothers to find and mate with females as rapidly as possible and then chew the exit tunnel. Little work has been conducted on male movement. Frank¹⁰ did find that males associated themselves during mating in a way consistent with the formation of brother bands, although he discussed alternative explanations. S. Maurice (pers. comm.) found that, in *Ficus citrifolia*, only a few of the males inside a syconium chew the exit hole, and they do so before all the females have been mated. Conducting experiments on these questions is simple¹⁰. Maintaining lines of wasps so that relatedness can be manipulated will be a valuable method in future work^{7,9}.

Little work has been done on the behavior and population dynamics of inquiline wasps. Hamilton¹⁶ reported some sex ratio data and stressed the widespread occurrence of fighting and wing polymorphism in males of

several species. Theory suggests that the number of inquiline females ovipositing in each syconium will influence the amount of sex ratio bias and wing polymorphism^{16,17}. The conditions leading to fighting, biased sex ratios, and wing polymorphisms are of general interest in evolutionary biology. Figs and their inquilines provide an excellent system for studying these problems (see Murray³¹ for an interesting study of male fighting, and Godfray¹² for interesting details on both pollinator and inquiline sex ratio and biology).

Conclusion

I have proposed several hypotheses about the ecological interactions among figs, pollinator wasps, and the many arthropod species associated with each fig species. These ecological interactions have a strong effect on fig reproductive success, often creating divergent selective pressures on male and female components of success. These selective pressures are, in turn, partly responsible for the evolutionary diversity of *Ficus* and its associated arthropods.

The observed diversity in fig traits invites speculation about the underlying developmental processes and selective pressures that have caused this variation. I have attempted to frame possible explanations in terms of both developmental and selective processes, and in a way that is amenable to empirical study. New hypotheses and future empirical work will be most useful if they simultaneously address developmental processes, components of reproductive success, and variation among species. These three types of data are, of course, what are needed for most kinds of evolutionary problems. Figs taunt seductively with the promise that all three types of data can readily be obtained.

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