A mutualism at the edge of its range

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

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

Introduction

Coevolved mutualisms can only persist in places that both partners can reach, and can survive and reproduce in once there. This simple constraint has profound consequences for the ecology and evolution of species dependent upon mutualists. Mutualisms (particularly obligate ones) commonly involve organisms of distant taxa, and their ecological requirements must often be widely divergent. A species whose mutualist is excluded from a given location may be unable to invade, may interact with an alternative partner, or may stop relying upon mutualists altogether, either on an ecological or evolutionary time scale. However, even if both partners are present, environmental conditions are likely to be more harsh for one of them. The success of the mutualism itself will therefore vary in space, as will selection pressures on it. Environment-specific selection pressures lead to the possibility of environment-specific adaptations over the range of a single mutualistic interaction. Few data are available on geographic variation within mutualisms, because these interactions have nearly always been studied at a single site. Even basic information about the components of a particular mutualistic interaction that are most sensitive to environmental variation is rare. My intention here is to review information on geographic and seasonal variation in the success of a primarily tropical mutualism, the fig/pollina-
The obligate interaction between figs (*Ficus* spp., Moraceae) and their pollinators (Hymenoptera: Agaonidae) is exceptionally common and widespread. There are probably over 700 species pairs worldwide. Figs and their pollinators evolved and are most abundant in the equatorial tropics, but representatives are present as distant as 45° north and 35° south latitude. (Detailed distributions are given by Berg). This mutualism offers three distinct advantages for studying patterns of geographical variation. First, the consequences of poor survival or reproduction of each mutualist are strong and straightforward: if fig trees of a given species fail to flower, their pollinators will rapidly die off, and if pollinators cannot survive the flight between trees, the trees will not set fruit. Second, it is easy to identify one aspect of environmental variation, namely seasonality, that should affect the success of both partners, and thus of their interaction. During cool periods, fig wasp survival and flight ability are strongly limited, and fig trees initiate flowering much more rarely. Lastly, a small but growing data base is available for studying patterns of variation in fig traits. Ecological studies have been carried out on about 50 species over a broad geographical range (fig. 1). In a few cases, the same fig-pollinator pair has been studied in different parts of its range; because the interaction itself is fairly stereotyped, comparisons can also be drawn (with caution) among groups of species pairs in contrasting regions.

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

**Factors regulating pollination/oviposition success**

A model of interacting fig and pollinator populations

The interaction between monoecious figs and their pollinators that is now considered 'typical' is based on the classic studies of *Ficus sycomorus* by J. Galil and D. Eisikowitch in East Africa. It can be summarized briefly as follows (table 1).

<table>
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<th>Phase</th>
<th>Description</th>
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<td>A (pre-female):</td>
<td>young syconium prior to the opening of the ostiole.</td>
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<tr>
<td>B (female):</td>
<td>ostiolar scales loosen, female flowers ripen, pollinators penetrate into the syconium and oviposit into the ovaries.</td>
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<tr>
<td>C (interfloral):</td>
<td>wasp larvae and fig embryos develop within their respective ovaries.</td>
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<tr>
<td>D (male):</td>
<td>male flowers mature, wasps reach the imago stage, fertilized female wasps leave the syconium via tunnels bored by the males.</td>
</tr>
<tr>
<td>E (post-floral):</td>
<td>both the syconium and the seeds inside them ripen.</td>
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</tbody>
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Pollen-carrying female wasps arrive at a tree bearing several hundred or thousand inflorescences, or syconia. Each one is a hollow structure (a multiple receptacle) lined with hundreds of florets. At the time the wasps arrive, only the female florets are receptive. The wasps enter the syconia via the ostiole, becoming trapped in the process. Once inside they deposit pollen on the stigmas, then oviposit directly into some of the ovaries. A mixture of seeds and seed-eating wasp larvae develops over the next several weeks. When the wasps are mature, they copulate. Females then collect pollen from the newly mature anthers, while males tunnel back through the wall of the fig. The female wasps then depart, in search of syconia in which to oviposit. As a rule, syconia on an individual tree are highly synchronized, whereas different trees flower out of synchrony. Therefore, the wasps must locate another tree in the correct sexual phase. They have little time in which to do so; free-living adults do not feed and survive several days at most.

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

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

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