CHAPTER 26

Rapid evolution of pollinator-mediated plant reproductive isolation

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26.1 Plant–insect diversification

When considering the tree of life, the fact that some lineages are much more taxonomically rich than others suggests that rates of species diversification are highly variable. Explaining patterns of species diversity according to changes in diversification rate is limited by our power to reconstruct patterns of speciation and extinction through time, but this has not deterred speculation on the rate of evolution in mega-diverse groups such as flowering plants and insects (Sanderson and Donoghue 1994; Farrell 1998). The role of specialized interactions between insect herbivores and their host plants has been especially popular in explaining insect diversity by coevolutionary processes (Ehrlich and Raven 1964; Farrell et al. 1992). That reproductive isolation of herbivore populations may arise due to specialization on novel plant hosts is illustrated by the apple maggot fly, *Rhagoletis pomonella,* which broadened its host range over the past 300 years from native hawthorn (*Crataegus*) to include the introduced apple (*Malus*) in North America (Feder et al. 1994). Yet examples of herbivore speciation as a consequence of adaptation to different host plants, such as soapberry bugs (Carroll and Boyd 1992) and pea aphids (Peccoud et al. 2010), rarely consider the rate of host plant diversification. The role of herbivores in affecting plant diversification may be intensified when herbivores also provide pollination services, and directly affect reproduction of the host plant. In this chapter we focus on conditions in which insect pollinators acting as agents of reproductive isolation could influence the rate of speciation in flowering plants.

26.2 Pollination and reproductive isolation

While examining orchids, Darwin hypothesized that coevolution between flowering plants and pollinators might be responsible for their correlated patterns of diversity (Darwin 1862). Overall patterns of angiosperm diversity suggest that elevated diversification rates might be associated with biotic pollination (Jesson 2007). However, critical evaluation of this hypothesis leads to the conclusion that biotic pollination is 'neither a necessary nor sufficient condition for large numbers of species' (Gorelick 2001). Recent meta-analysis (Vamosi and Vamosi 2010) attributed episodes of angiosperm diversification primarily to geography, or 'space to diversify,' and only secondarily to biotic pollination. Given the limitations of such broad comparisons and correlative methods in identifying evolutionary processes, we focus on particular systems in which (and mechanisms by which) pollinators are implicated in accelerated plant diversification.

The role of pollinators as agents of selection on floral traits and the idea that pollinator specialization on divergent floral forms could result in the reproductive isolation of plant varieties gained broad acceptance during the 20th century (Grant 1949; Kiester et al. 1984; Johnson et al. 1998). Nonetheless, there are few specific cases of increased plant diversification attributed to pollinator interactions (Hodges et al. 2004; Sargent 2004).

Pollinator foraging behavior has repeatedly been shown to play a role in plant reproductive isolation through constancy of floral visitation (Kephart and Theiss 2004). Modes of pollen transfer have also been implicated. For example, floral symmetry restricts the approach and movement of pollinators such that pollen placement may be precise and further reduces the likelihood of interbreeding among dissimilar floral forms (Sargent 2004). Floral mechanical means of reproductive isolation has been documented in species-rich groups such as orchids (Sun et al. 2011), gingers (Kay 2006), and louseworts (Yang et al. 2007). However, it is difficult to discern whether such mechanisms are causes or consequences of diversification if we admit the possibility of selection for traits reduces the likelihood of interbreeding when hybrids are less fit (e.g. reinforcement). In this chapter, we describe a system in which reinforcement appears unlikely and that also happens to meet conditions for rapid, pollinator-mediated speciation. Simple models predict pollinator-mediated plant diversification in the case of obligate mutualisms with highly host-specific pollinating seed predators where plant and pollinator reproduction are closely coupled (Kiester et al. 1984). The fig–fig wasp mutualism not only meets these criteria, but molecular phylogenetic studies (Datwyler and Weiblen 2004) have established the evolutionary historical context necessary for comparing diversification rates.

26.3 *Ficus* versus Castilleae

The recently discovered sister group relationship of figs (*Ficus*) to the tribe Castilleae (Moraceae) provides the opportunity to compare extant diversity and infer conditions associated with changes in diversification rate. Sister-group comparison may provide insights on such conditions given that these lineages share similar floral traits, modes of pollination, and time since divergence from their most recent common ancestor at least 65 million years ago (Zerega et al. 2005). Wind pollination is the inferred ancestral condition of the mulberry family (Moraceae) with a hypothesized shift to biotic pollination in the most recent common ancestor of *Ficus* and Castilleae (Datwyler and Weiblen 2004). Associated with the transition from wind to insect pollination were morphological changes in the position of flowers within inflorescences, particularly the arrangement of bracts that encircle the flowers of each inflorescence (Clement and Weiblen 2009). Whereas *Ficus* is one of the largest and most ubiquitous plant genera in tropical and subtropical forests with more than 800 species worldwide, Castilleae spans the same habitats and geographic range but comprises 11 genera and only ~60 species in total. This tenfold difference in species richness cannot be solely attributed to the shift from wind to biotic pollination in the common ancestor. But rather, we must consider other ecological or evolutionary differences among the descendants. Along the continuum of generalization and specialization in plant–pollinator interactions, brood-site pollination mutualisms involving insects are the most extremely specialized (Waser and Ollerton 2006). Recent ecological studies (Sakai 2001; Zerega et al. 2004; Clement 2008) have uncovered an insect brood-site pollination syndrome similar to that of figs throughout the geographic distribution of Castilleae. The evolution of a specialized brood-site pollination syndrome from a more conventional and generalized mode of insect pollination therefore does not appear to account for the richness of *Ficus* relative to Castilleae. In seeking to explain the tenfold difference in numbers of species between sister clades, we describe their pollination ecology in detail and conditions affecting the evolution of reproductive isolation in particular.

Ficus is characterized by a completely enclosed inflorescence, or syconium, which is the site of the obligate mutualism with pollinating fig wasps (Agaonidae, Hymenoptera). The urn-shaped receptacle bearing numerous unisexual flowers is closed at the apex by involucral bracts that form a narrow passage, or ostiole, which is only accessible to certain agaonid wasps (Fig. 26.1). The agaonid life cycle begins and ends in syconia, where galled pistillate flowers nourish larvae, and mating occurs in the fig cavity immediately upon eclosion. Female wasps collect pollen from staminate flowers, emerge from ripening syconia, and search for receptive syconia in which to oviposit. Floral volatiles and agaonid chemosensory antennae are involved in locating and choosing hosts. Access to potential brood sites requires passage through the

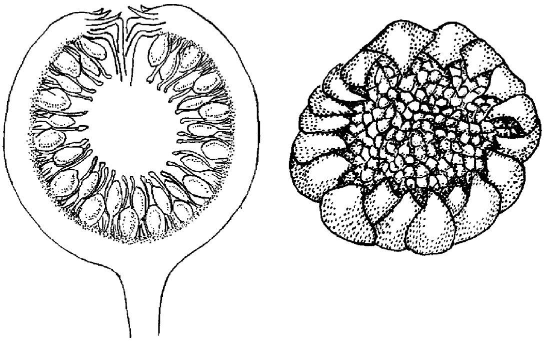

Figure 26.1 Inflorescence morphology of *Ficus* and Castilleae (Moraceae). The fig, or syconium (left), completely encloses the flowers within a hollow receptacle accessible only through a bract-lined opening, or ostiole. The staminate inflorescence of *Antiaropsis decipiens* (Castilleae, right) is discoid and has dozens of tightly packed flowers surrounded by involucral bracts. The illustration for *Ficus* first appeared in Whitfeld and Weiblen (2010) in *Harvard Papers in Botany* **15**: 1–10 and is reprinted here with permission of the editors of *Harvard Papers in Botany.* The illustration for *Antiropsis* first appeared in (Zerega et al. 2004) (© University of Chicago 2004).

ostiole where involucral bracts strip the wings and antennae of agaonids such that the syconium generally entombs each floral visitor. As agaonids lay eggs in a fraction of the pistillate flowers, pollination may be either active or passive but in either case, the development of seeds and galls is assured.

The specialized nature of fig/pollinator interactions has made the system a focal point for studies of coevolution (Herre 1989; Ganeshaiah et al. 1995; Weiblen 2004; Ma et al. 2009). Each *Ficus* species is associated with one or several pollinating fig wasp species (Herre et al. 2008) and approximately parallel patterns of phylogenetic diversity among more than 800 taxa has drawn much speculation on processes of diversification (Weiblen and Bush 2002; Machado et al. 2005; Jackson et al. 2008; Jousselin et al. 2008). Whether diversification is the result of cospeciation, host switching, or hybridization, the intertwining of fig and pollinator life cycles is implicated. When life cycles are linked, specificity has the potential to influence reproductive isolation of diverging populations in several ways. Among the possibilities are chemosensory responses of pollinators to fig volatiles (Grison-Pige et al. 2002), navigation of ostiolar bracts according to pollinator head shape (van Noort and Compton 1996), gall and seed formation as mediated by the interaction of the ovipositor with floral morphology (Weiblen 2004), variation in larval performance among hosts, and pollen compatibility. We will argue that interactions which are lacking in the Castilleae brood-site pollination mutualism could affect the rapid evolution of reproductive isolation in pollinators and figs simultaneously.

Compared to syconia, the inflorescences of Castilleae are discoid or urn-shaped (Sakai 2001; Clement and Weiblen 2009) but the receptacle does not completely enclose the flowers (Fig. 26.1). Inflorescences are unisexual with either stigmas or stamens protruding beyond the involucral bracts of pistillate and staminate inflorescences, respectively (Datwyler and Weiblen 2004). Although studies of fig pollination are more numerous, all reports of Castilleae pollination from each major tropical region involve thrips (Thysanoptera) (Sakai 2001; Zerega et al. 2004; Clement 2008). Thrips feed on pollen at all life stages and only incidentally pollinate in the course of foraging, but they are known to breed in flowers and can be highly host-specific (Mound 2005). In the case of Castilleae, pistillate inflorescences provide no reward such that pollination involves deceit by floral mimicry. Thrips lay eggs prior to anthesis in the relatively short-lived staminate inflorescences, where nymphs later feed on pollen and eventually pupate in fallen litter. Unlike fig wasps, thrips feed as adults and move between plants while foraging and seeking opportunities for mating and oviposition. Thrips are predominantly associated with staminate inflorescences of Castilleae but the similar appearance and odor of pistillate inflorescences attracts occasional thrips where passive pollination of exposed stigmas is sufficient to affect fertilization (Zerega et al. 2004; Clement 2008). The fact that individual adult thrips have an opportunity to visit flowers in multiple inflorescences whereas fig wasps are limited to visiting a single inflorescence per generation is a key difference between pollination syndromes, possibly affecting the evolution of reproductive isolation and the rate of host plant speciation.

Differing extinction rates provide an alternative explanation for the relatively greater richness of *Ficus* but there is little reason to expect that Castilleae are more extinction-prone. The groups share identical habitats and pan-tropical geographic distributions. The complete enclosure of flowers within the syconium that severely limits opportunities for pollination favors fig species as more likely candidates for extinction than Castilleae. We argue that a higher rate of speciation in *Ficus*, due to particular conditions of the pollination syndrome, promotes the rapid evolution of reproductive isolation and explains why figs outnumber their sister group in species by ten to one. Species-specificity and floral constancy of pollinators are often invoked as reproductive isolating mechanisms in plants (Waser and Ollerton 2006). The discovery of thrips as primary pollinators of Castilleae, comprising not only greater than 95% of visitors to inflorescences but also exhibiting one-to-one host species-specificity in Panama and Papua New Guinea (Sakai 2001; Zerega et al. 2004), indicates a degree of specialization that appears rather similar to fig pollination. A closer examination of life history differences between these brood-site pollination syndromes is needed to identify conditions beyond species-specificity that favors more rapid evolution of pollinator-mediated reproductive isolation in figs than Castilleae.

Here we elaborate on two conditions that appear likely to have accelerated fig diversification relative to Castilleae. The first involves the nature of the reward for pollination services. Although both systems provide brood sites, fig wasps are seed predators whereas thrips are pollen feeders. Fig pollination enhances pollinator fitness by provisioning seed resources to offspring in galled pistillate flowers whereas pollination of Castilleae does not directly contribute to thrips fitness. A fig that hosts the offspring of a particular pollinator also achieves fitness through the attraction of that pollinator such that gene flow in fig populations is closely coupled with the reproductive consequences of wasp host choice. In dioecious Castilleae, however, thrips oviposition and pollen feeding only occur on non-pollinated plants such that the female component of plant fitness is not positively associated with foraging for brood sites. Whether fitness consequences of host choice by floral visitors are closely coupled with pollination or not may influence the rate by which plant reproductive isolation evolves if an additional condition is met.

The second condition for rapid plant speciation has to do with the number of floral visits per pollinator generation. Because fig wasps visit only a single inflorescence per generation, host choice has more immediate fitness consequences for fig wasps than for thrips. Once a fig wasp has located a host fig and entered the ostiole, her reproductive success is completely dependent on the suitability of that particular host whereas thrips have the option of bet hedging with visits to multiple inflorescences. The existence of ″tomb blossoms,′ especially in functionally dioecious *Ficus* species having ‘female’ figs in which pollinators absolutely fail to achieve fitness, may impose intense selection on wasps to discern host quality prior to passing the ostiole. Recent manipulative pollination experiments with functionally dioecious figs documented the complete failure of pollinators to reproduce in sympatric, close relatives of a preferred host species (Moe 2011). Whereas visiting the wrong host imposes an absolute fitness cost to a fig wasp, thrips visiting suboptimal hosts, such as the pistillate infloresences of Castilleae that provide no reward, at least affords the possibility of locating a more suitable host with subsequent foraging. Positive selection for highly discriminatory host choice in response to the volatile chemical attractants of receptive figs is consistent with extremely species-specific patterns of fig/pollinator association (Bronstein 1987; Weiblen et al. 2001), the low incidence of pollinator sharing among sympatric fig species (Weiblen et al. 2001; Moe et al. 2011), and the apparent rarity of natural hybrids in at least some fig lineages (Parrish et al. 2003; Moe 2011). Such selection on fig wasps sets the stage for the rapid evolution of reproductive isolation in the host species.

26.4 A pollinator-mediated model for fig speciation

The obligate association of mutualistic partners (Fig. 26.2) sets conditions such that the discriminatory behavior of floral visitors is sufficient for plant reproductive isolation in the absence of postzygotic mechanisms such as pollen incompatibility, hybrid inferiority, or infertility. Crossing experiments recently demonstrated that closely related fig species are interfertile and that hybrid seedlings grow at rates comparable to non-hybrids (Moe 2011). There are also numerous anecdotal reports of fig hybrids in nature (Parrish et al. 2003; Machado et al. 2005; Moe 2011) However, manipulative experiments bypassing the host recognition phase of the pollinator life cycle found that the offspring of pollinators which successfully galled novel host species did not develop to maturity (Moe 2011). These observations together suggest that reproductive isolation among fig populations depends less upon postzygotic mechanisms and more upon pollinator fitness consequences of attraction to fig volatile chemistry. Given that wasp generation times are at least an order of magnitude shorter than those of their host trees (Fig. 26.2), the wasp chemosensory apparatus and associated behaviors are also likely to evolve more rapidly than postzygotic isolating mechanisms in host figs. We argue that the evolution of prezygotic reproductive isolation is driven by the wasp olfactory response that, according to the results of manipulative experiments, is selected for attraction to figs similar to that of the natal fig. Variation in volatile chemical bouquets introduced into a fig population through mutation, migration, hybridization, or even nongenetic factors such as local soil conditions or microbial interactions has the potential to become a target for discrimination that could effectively achieve reproductive isolation among variant subpopulations within a few generations (Fig. 26.3). The divergence of fig subpopulations, either by genetic drift or local adaptation, is expected to lag behind that of pollinator host race formation according to differences in generation time but is nonetheless expected to outpace that of Castilleae where selection for pollinator discriminatory behavior is neither so intense nor positively associated with pollination.

The proposed model finds obvious application in fig/pollinator associations characterized by extreme host specificity and congruent cophylogenetic patterns (Weiblen and Bush 2002) but it also applies to alternative modes of speciation. Pollinator sharing among fig species (Molbo et al. 2003), incongruent fig and pollinator phylogenies (Machado et al. 2005), and cyto-nuclear discordance indicative of fig hybridization (Renoult et al. 2009) suggest that host-switching may also be an important mechanism of diversification in this system (Herre et al. 2008). Hybridization has the potential to generate novel profiles of chemical attractants and new targets for discriminatory pollinators such that a hybrid fig, once colonized by a pollinator whose offspring prefer similar hosts, could found a

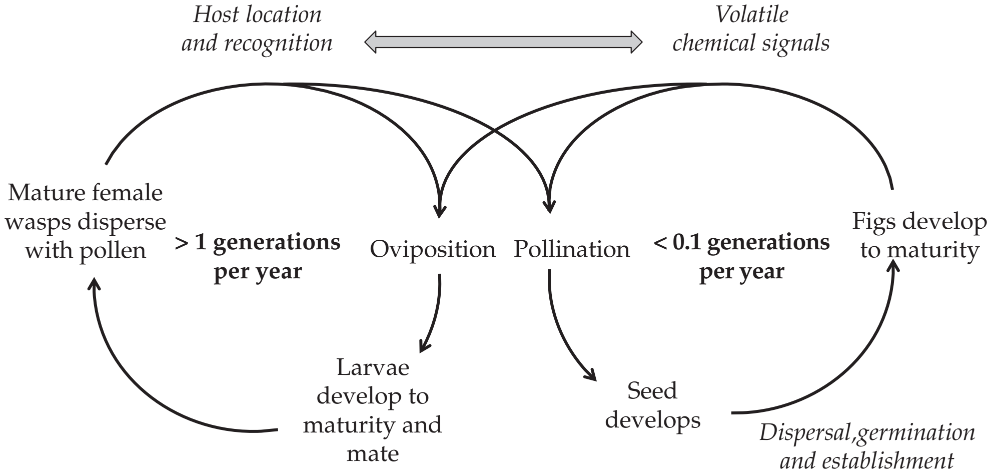

Figure 26.2 Intersecting life cycles of figs and fig wasps. The evolutionary dynamics of reproductive isolation are likely to involve genes affecting the production of volatile chemical signals by figs and their recognition by wasps. Genes affecting the success of oviposition, pollination, seed and larval development are also likely to be important. Due to the interplay of relatively shorter wasp generation times with longer fig life cycles, selection acting on wasp genetic systems and/or the evolution of reproductive isolation among wasp populations may increase the rate of speciation in figs.

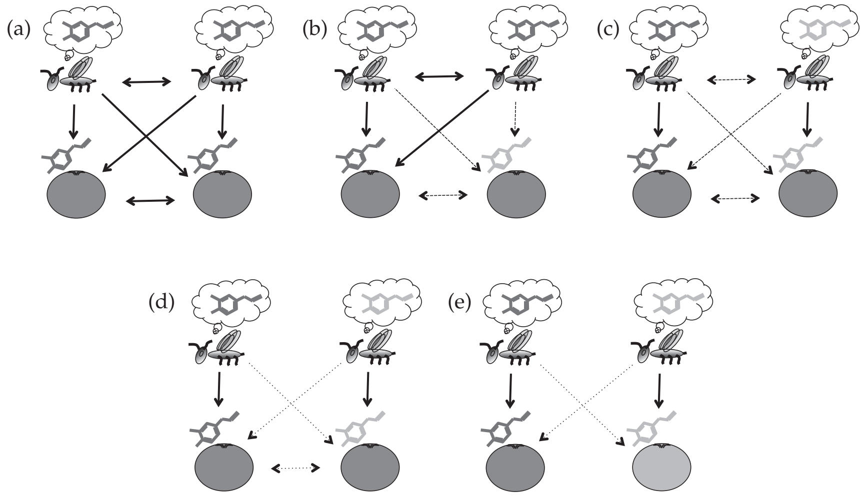

Figure 26.3 A model for the rapid evolution of pollinator-mediated reproductive isolation in figs. Horizontal arrows represent gene flow. Vertical and diagonal arrows represent plant/pollinator interactions. Solid arrows indicate frequent events whereas dashed arrows indicate rare events. (a) Host population with individuals having volatile bouquets with equal probability of attracting pollinators. (b) Variant fig arises with initial low probability of attracting pollinators. (c) Once colonized, the probability of the new variant attracting specific pollinators increases, given that wasps prefer volatiles similar to that of their birth fig. (d) Preference of pollinators for different variants leads to assortative mating, reproductive isolation, and speciation of pollinator host races. (e) Host plant speciation lags behind pollinator speciation due to longer generation times.

new lineage capable of exploiting ecological niches inaccessible to the parental species within a few generations (Gross and Rieseberg 2005). Evidence from fig wasp phylogeography (Haine et al. 2006; Moe and Weiblen 2010) suggests allopatric speciation where geographic variation in fig volatile profiles could also contribute to the rapid evolution of pollinator-mediated reproductive isolation. A next step in validating the proposed model and investigating its generality would be to examine the molecular evolution of genes affecting the fig wasp chemosensory apparatus and fig volatile chemistry in diverse fig/pollinator lineages and geographic contexts.

26.5 Future directions: plant–pollinator interactions and rapid evolution

The coupling of plant and pollinator life cycles may accelerate plant speciation under certain conditions. Given the continuum of variation from specialized to generalized animal-pollinated systems, it seems unreasonable to expect diversification in biotic pollination systems to be elevated relative to abiotic pollination overall. Comparisons of highly specialized systems similar to fig pollination are needed to gain further insights on conditions for rapid, pollinator-mediated plant diversification. Speciation in figs appears to be accelerated through: (1) the linkage of plant and pollinator reproduction, (2) severe pollinator fitness consequences for ‘mistakes’ such that highly discriminatory behavior is selected, and, (3) substantially shorter generation times in pollinators than in host plants. It will be necessary to examine these criteria in other brood-pollination mutualisms involving yucca and yucca moths (Pellmyr 2003), senita cactus and senita moths (Fleming and Holland 1998), and phyllanthoid euphorbs and *Epicephala* moths (Kato et al. 2003). For instance, *Yucca* is not more rich in species than its wind-pollinated sister group (Smith et al. 2008). Although plant and pollinator reproduction are also linked in yucca pollination, and moths have substantially shorter generation times than their hosts, moths may visit flowers of multiple plants such that the consequences of suboptimal choices are not as severe as for fig wasps. Such comparisons may shed light on whether the evolution of pollinator-mediated reproductive isolation has matched plant speciation by polyploidy or hybridization in rapidity and extent.

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