

Selection by Pollinators and Herbivores on Attraction and Defense

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Interactions between plants, their herbivores, and their pollinators are thought to have led to the diversification of both plants and insects. Historically, studies of plant-herbivore and plant-pollinator interactions have occurred independently. Research at both micro- and macroevolutionary levels has focused on the evolution of plant resistance in the context of herbivory, and on floral traits in the context of pollination. For example, researchers have long recognized the role of plant secondary chemicals in herbivore feeding preferences (e.g., Dethier 1941). Fraenkel (1959) proposed that the “reason for existence” of plant secondary chemicals was to attract and deter herbivores rather than as products of plant metabolism, building on earlier work by Stahl (1888) and others. Ehrlich and Raven’s classic article (1964) on coevolution concluded that “the evolution of secondary plant substances and the stepwise evolutionary responses to these by phytophagous organisms have clearly been the dominant factors in the evolution of butterflies and . . . in the evolution of angiosperm subgroups” (p. 382). This publication and others in the 1970s (e.g., Feeny 1976; Rhoades and Cates 1976) led to a surge of interest in chemical defenses mediating plant-herbivore interactions. More recently, selection on plant resistance traits has been studied by manipulating herbivores as selective agents (e.g., Mauricio and Rausher 1997; Stinchcombe and Rausher 2001), and several phylogenetic studies interpret the diversification of plants and herbivores in the context of coevolution mediated by plant resistance traits (e.g., Farrell et al. 1991; Becerra 1997, 2003; Farrell and Mitter 1998; Cornell and Hawkins 2003).

By contrast, the diversity of plant floral traits has been interpreted as the result of evolution due to their obvious role in attracting pollinators and promoting efficient pollination. Sprengel’s 1793 pioneering treatise (first translated to English in 1996) interpreted floral function in terms of relationships with pollinators and inspired much of the sub-

sequent field of pollination ecology. Darwin also interpreted the floral morphological variation of heterostylous plants in terms of its role in promoting outcrossing (Darwin 1877). More recently, pollination biologists have suggested that the evolution of floral traits may be shaped by a diversity of pollinators, rather than a single pollinator or guild type (e.g., Herrera 1996; Waser et al. 1996). Recent theoretical models and manipulative studies continue to focus on the role of pollinators in shaping the evolution of floral traits (e.g., Dafni and Kevan 1997; Aigner 2001; Fenster et al. 2004) and on floral trait phylogenetic diversity in the context of pollinator attraction and efficiency (e.g., Jurgens 2004; Sargent and Otto 2004; Manning and Goldblatt 2005; Ree 2005).

Clearly, herbivores have been a major selective force in the evolution of plant defense, and pollinators have been a major selective force in the evolution of attractive floral traits. However, a growing number of studies suggest that traits that deter herbivores may affect pollinator attraction, and traits that attract pollinators may affect herbivores. Herbivores and pollinators could exert selection on plant traits either through direct interactions (a pairwise relationship between plants and insects mediated by the trait), or via indirect interactions (insect selection on plant traits that is mediated by a third species) (Wootton 1994). Over half a century ago Grant (1950) recognized that floral morphology may have evolved to protect ovules from damage by some pollinators, such as birds and beetles, as well as to promote pollen transfer. More recent phylogenetic studies demonstrate that floral traits have evolved in response to selection from both pollinators and herbivores (e.g., Armbruster 1997; Armbruster et al. 1997; Pellmyr 2003). For example, resin-secreting floral glands that defended flowers of *Dalechampia* vines were subsequently co-opted as a reward for resin-collecting pollinating bees (Armbruster 1997). Thus, the evolution of plant traits may be shaped by

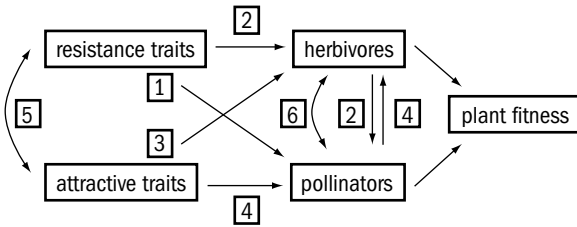


FIGURE 12.1. Paths by which plant resistance and attractive traits could affect plant fitness via interactions with herbivores and pollinators. This conceptual framework could be extended to other antagonist and mutualist interactions. Numbers refer to corresponding text sections discussing each pathway: 1, “Direct Effects of Resistance on Pollinators”; 2, “Indirect Effects of Resistance on Pollinators”; 3, “Direct Effects of Attractive Traits on Herbivores”; 4, “Indirect Effects of Attractive Traits on Herbivores”; 5, “Resistance and Attraction Traits May Not Be Independent”; 6, “Herbivores and Pollinators May Not Be Independent.”

simultaneous or sequential interactions with both pollinators and herbivores.

Attractive and defensive traits can be genetically correlated via linkage or pleiotropy. Thus herbivore-imposed selection on resistance may drive the evolution of floral traits and vice versa. Furthermore, herbivores and pollinators themselves are not independent of each other. Several insect taxa include species that are pollinators as adults and herbivores as larvae. Traits that attract adult pollinators therefore have the potential to increase subsequent herbivory in some systems. The consequence of these interactions for plant fitness will depend on the level of specialization and on community context. For example, a pollinating herbivore may benefit plants when other pollinators are unavailable, but reduce plant fitness when nonherbivorous pollinators are also present (Thompson and Cunningham 2002).

Abiotic factors as well as community context can alter the expression of traits and the fitness consequences of interactions. Pathogens and soil microorganisms may also play a large role in the evolution of plant traits (e.g., Agrawal et al. 1999) but are outside the scope of this book. Furthermore, many secondary compounds serve functions other than defense, such as UV protection and the oxidation of free radicals (e.g., McCloud and Berenbaum 1994; Izaguirre et al. 2003; Gould 2004). For simplicity, I consider here just the role of insects on the evolution of attractive and defensive traits, while acknowledging that other factors undoubtedly play significant roles in the evolution of these traits.

In this chapter, I review the literature on selection by pollinators and herbivores on resistance and attractive traits, with the goal of highlighting the pathways by which pollinators may affect the evolution of plant resistance, and herbivores may affect the evolution of floral attractive traits. Figure 12.1 provides a schematic diagram, with numbered paths referring to corresponding sections in the text.

Selection by Pollinators on Plant Resistance

Direct Effects of Resistance on Pollinators

Resistance to herbivores may incur a variety of costs for plants, including ecological costs of deterring other mutualists (Strauss et al. 2002). A small but growing number of studies have shown that resistance traits may have direct, negative impacts on pollinator preference. For example, *Brassica rapa* lines that were artificially selected for high myrosinase (i.e., high herbivore resistance) produced flowers with smaller petals and were less attractive to pollinators compared to low-resistance lines (Strauss et al. 1999). Such aversion could be due to the expression of defensive traits in flowers, or to defense costs resulting in reduced allocation to floral traits. Other systems have shown that resistance to floral antagonists can deter pollinators. Floral spines deterred nectar thieves but also reduced pollinator time per visit in *Centaurea solstitialis* (Agrawal et al. 2000), and nectar alkaloids in *Gelsemium sempervirens* deterred nectar robbers at a cost of reduced pollinator attraction (Adler and Irwin 2005). Additionally, if floral antagonists and pollinators prefer the same phenotypes, they may exert opposing selection on floral traits (Gomez 1993; Eriksson 1995; Ehrlen 1997). For example, floral seed predators and pollinators exerted opposing selection pressures on calyx length in *Castilleja linariaefolia* (Cariveau et al. 2004) and scape length in *Primula farinosa* (Ehrlen et al. 2002), and predispersal seed predators and pollinators may exert opposing selection on flowering phenology and inflorescence size in *Ipomopsis aggregata* (Brody 1997; Brody and Mitchell 1997). Thus, if pollinator attraction affects plant fitness, pollinators may select against resistance traits expressed in flowers or traits that cause reduced allocation to floral display or rewards.

In some cases plants may circumvent the negative effects of resistance on pollinators. For example, *Acacia* trees produced a volatile that deterred guarding ants from “protecting” young flowers against pollinators (Willmer and Stone 1997), and corollas of *Nicotiana attenuata* increased pools of the attractant benzyl acetone and decreased pools of nicotine at dusk, when *Manduca* spp. pollinators are most active (Euler and Baldwin 1996). However, when selection for increased defense in one tissue has pleiotropic consequences for expression in other tissues, plants may not be able to simultaneously evolve optimal solutions for attracting pollinators and deterring herbivores.

Indirect Effects of Resistance on Pollinators

Although herbivore resistance may directly deter pollinators, pollinators could select for higher levels of plant resistance by preferring undamaged plants. This indirect effect seems most probable when damage occurs on floral tissues, since floral cues are most likely to be used by pollinators to assess rewards. Damage to vegetative or even root tissue could also affect pollinator attraction. The effects of damage

to each of these tissues (floral, vegetative, and roots) are reviewed below.

Damage to floral tissue or consumption of floral resources (collectively referred to as floral antagonism) can reduce pollinator attraction. For example, florivory reduced pollinator preference and plant male or female reproduction in several systems (Lohman and Berenbaum 1996; Krupnick and Weis 1999; Krupnick et al. 1999; Mothershead and Marquis 2000; Adler et al. 2001). Florivory can also alter sex expression (Hendrix 1984). For example, a lepidopteran herbivore preferentially consumed more exerted floral parts in the distylous vine *Gelsemium sempervirens*, so that long-styled plants became functionally male and long-filamented plants became functionally female (Leege and Wolfe 2002). Florivory can also change sex allocation in future flowers via compensatory reproduction as a tolerance mechanism (Hendrix and Trapp 1981). Nectar robbing may reduce plant fitness indirectly by deterring pollinators (e.g., Irwin and Brody 1998, 1999, 2000), although robbing is not costly in all systems (reviewed in Maloof and Inouye 2000; Irwin et al. 2001).

Although floral antagonism reduced pollinator attraction and plant reproduction in several systems, few studies have elucidated traits conferring resistance to floral antagonists. Natural and artificial flower damage in *Nemophila menziesii* induced resistance to florivory in younger flowers (McCall 2006), but the responsible traits are unknown. Defensive compounds have been detected in flowers (Detzel and Wink 1993; Euler and Baldwin 1996; Zangerl and Rutledge 1996; Adler and Wink 2001; Gronquist et al. 2001; Strauss et al. 2004; Irwin and Adler 2006), pollen, and nectar (reviewed in Adler 2000; also Gaffal and Heimler 2000; Thornburg et al. 2003). Such compounds may provide the basis for resistance to floral antagonists, but this has generally not been demonstrated (but see Gronquist et al. 2001). Other floral traits, such as corolla shape (Galen and Cuba 2001), exposure of sexual organs (Leege and Wolfe 2002), nectar concentration (Irwin et al. 2004), pollen nutritional content or defenses (Adler 2000; Roulston and Cane 2000), and escape in time or space (Irwin et al. 2001, 2004; Theis et al. 2006a), could potentially be under selection by pollinators through conferring resistance to floral antagonists. Flower number may also influence resistance to floral predators. Two hundred years after *Silene latifolia* escaped floral antagonists by invading North America from Europe, North American lineages produce more flowers than European lineages (Blair and Wolfe 2004); these lineages may also be more attractive to pollinators.

In most cases, leaf herbivory reduced plant fitness by deterring pollinators (Strauss et al. 1996; Lehtila and Strauss 1997; Strauss and Armbruster 1997; Mothershead and Marquis 2000; Hamback 2001; Poveda et al. 2003), although there can be differential effects on male compared to female fitness (Strauss et al. 2001). Leaf herbivory generally reduced floral traits associated with both male and female fitness. Simulated diabroticite beetle damage to *Cucurbita texana*

branches reduced the number of male flowers, the amount of pollen per flower, and pollen siring success (Quesada et al. 1995). Vegetative herbivory in a variety of systems reduced flower number, size, height, and flowering period (Karban and Strauss 1993; Lehtila and Strauss 1997, 1999; Mothershead and Marquis 2000; Hamback 2001; Poveda et al. 2003, 2005b; Ivey and Carr 2005), and pollen and nectar production, quality, or exertion (Lehtila and Strauss 1999; Ivey and Carr 2005; Poveda et al. 2005b). Vegetative herbivory can also alter plant sex ratio (Hendrix and Trapp 1981; Hendrix 1984; Krupnick and Weis 1998; Krupnick et al. 2000; Thomson et al. 2004) and mating system (Elle and Hare 2002; Steets and Ashman 2004; Ivey and Carr 2005).

Links between belowground herbivory and pollination are only beginning to be explored. Surprisingly, root herbivory may increase pollinator attraction (Poveda et al. 2003, 2005a), although the mechanism is not clear (Poveda et al. 2005b). Belowground herbivory may also attract other aboveground mutualists. Root herbivory reduced inflorescence size in thistles, but increased attraction of both tephritid seed predators and their parasitoids (Masters et al. 2001). Artificial and natural root herbivory in greenhouse cotton increased extrafloral nectar production, which was interpreted as an induced indirect defense to attract natural enemies (Wackers and Bezemer 2003). If these studies represent general patterns, pollinators or other aboveground mutualists have the potential to select for reduced resistance to belowground herbivory. However, very little is known about the mechanisms or genetic basis of root resistance to herbivory (but see Davis and Rich 1987; Zangerl and Rutledge 1996; Rasmann et al. 2005 for examples); this is clearly an open area for future research.

This review demonstrates that resistance traits may directly deter pollinators, but such traits can also indirectly attract pollinators by reducing herbivory. Ultimately, the net result of pollinator selection on resistance will depend on (1) the importance of pollinator service for plant fitness, and (2) the relative importance of direct deterrence versus indirect attraction of pollinators to resistant plants.

Selection by Herbivores on Floral Traits

Direct Effects of Attractive Traits on Herbivores

Attractive floral traits have the potential to directly attract herbivores as well as pollinators. This conflict is analogous to the trade-off between natural and sexual selection that is commonly studied in the animal kingdom, where individuals signal to attract mates, but such signals can also attract predators (e.g., Tuttle and Ryan 1981). In plants, floral signals and rewards may attract a variety of antagonists that consume floral resources, as well as pollinators. *Ipomopsis aggregata* plants with larger inflorescences, for example, attract higher rates of predispersal seed predation (Brody and Mitchell 1997), and *Polemonium viscosum* plants with wider corollas were more attractive to nectar-robbing ants

in addition to bumblebee pollinators (Galen and Cuba 2001). Several floral traits including flower production affected resistance to the bud-clipping weevil *Anthonomus signatus* in strawberry, *Fragaria virginiana* (Ashman et al. 2004). Male plants were less resistant and more tolerant of herbivory compared to hermaphrodite plants. Within males, plants with higher pollen production had more herbivory, suggesting that pollen production could be under selection by both pollinators and herbivores. Scent also attracts herbivores as well as pollinators. *Cucurbita* species that have more fragrant flowers attract higher numbers of *Diabrotica* pollen-feeding beetles (Andersen and Metcalf 1987), and two floral volatiles attracted both pollinators and floral herbivores in *Cirsium arvense* (Theis 2006). The timing of scent emission may reflect selection to attract pollinators while avoiding florivores (Euler and Baldwin 1996; Theis and Raguso 2005; Theis et al. 2006b). In cases where floral antagonists and pollinators prefer the same floral traits, plants may experience conflicting selection pressures to maintain pollinator attraction while resisting herbivores.

In some cases, leaf herbivores may be attracted to plants by floral or extrafloral resources. This can happen when herbivores have a wide diet, including nectar or pollen in addition to leaf material. Alternatively, insects may consume nectar or pollen as adults but leaf or vegetative tissue as larvae. For example, domestic cotton varieties with extrafloral nectaries experience greater levels of herbivory from a variety of hemipteran and lepidopteran larvae whose adults feed on the nectar (Lukefahr and Rhyne 1960; Schuster et al. 1976; Flint et al. 1988; Scott et al. 1988). Such a trade-off may also exist for extrafloral nectar production in wild cotton (Rudgers 2004; Rudgers and Gardener 2004). In these cases, adults are not pollinators, and the outcome of the interaction is negative from the plant's perspective. Cases in which adult pollinators have herbivorous larvae are reviewed below (see "Herbivores and Pollinators May Not Be Independent"). In either circumstance, one of the consequences of advertising or producing floral or extrafloral rewards may be attraction of herbivores. When herbivory reduces plant fitness and attractive traits are heritable, such traits may evolve in response to herbivory as well as pollination.

Indirect Effects of Attractive Traits on Herbivores

The attraction of pollinators could benefit some herbivores such as seed predators, because seed predators require fruit set for larval survival. Seed predators that oviposit before pollination should prefer attractive flowers to increase the chances of locating a future fruit for their offspring (e.g., Brody and Morita 2000). Even seed predators that oviposit after pollination may choose plants with the highest fruit production, which may correlate with previously expressed attractive traits. For example, plants with larger inflorescence heads had higher incidences of predispersal seed predation both within and across species of Asteraceae. Thus, inflorescence size might represent a trade-off between

attracting pollinators versus seed predators (Fenner et al. 2002).

Floral traits may also attract natural enemies that reduce herbivory. Many adult parasitoids feed on nectar (Kidd and Jervis 1989) and are particularly attracted to flowers with open corollas and easily accessible nectar (Patt et al. 1997; Tooker and Hanks 2000). Adding nectar sources in crop plantings alters parasitoid behavior and may help control pest herbivores (reviewed in Patt et al. 1997; Baggen and Gurr 1998). Furthermore, nectar sugar composition, scent, and accessibility can all affect parasitoid learning and preference (Patt et al. 1997, 1999; Wackers 1999, 2001), and such traits may be under selection if they reduce herbivory. However, the benefit of nectar via attracting parasitoids may be balanced by the cost of attracting herbivores. For example, access to buckwheat (*Fagopyron esculentum*) and dill (*Anethum graveolens*) flowers increased longevity and fecundity of the encyrtid wasp parasitoid *Copidosoma koehleri* and its host, the gelechiid moth *Phthorimaea operculella*, whose larvae are pests on potato. By contrast, flowers of *Phacelia* and *Nasturtium* benefited the parasitoid but not the herbivore (Baggen et al. 1999). If findings from agricultural settings hold in natural environments where communities may be more complex, then accessibility or quality of floral nectar may provide an additional benefit to plants by attracting parasitoids that reduce herbivory. Such benefits will be greatest for plants when parasitoids kill eggs or early larval stages (idiobiont parasitoids) rather than late larval or pupal stages (koinobiont parasitoids).

Finally, pollinator attraction in one generation may be linked with plant-herbivore dynamics in the next. Progeny of selfed plants of *Mimulus guttatus* had lower resistance (Carr and Eubanks 2002) and tolerance (Ivey et al. 2004) to herbivory compared to progeny of outcrossed plants. These results suggest that traits attracting pollinators could influence plant-herbivore interactions in the offspring, if pollinator attraction affects outcrossing rates.

Resistance and Attraction Traits May Not Be Independent

A growing number of studies indicate that the expression of attractive and resistance traits are not independent. Traits such as floral resins, which evolved as herbivore defenses, can be co-opted over evolutionary time as pollinator rewards (Armbruster et al. 1997). In ecological time, the same trait can serve as both pollinator attractant and defense against florivory, such as production of ultraviolet pigments in *Hypericum calycinum* or showy bracts in *Dalechampia* species (Armbruster and Mziray 1987; Armbruster 1997; Gronquist et al. 2001). Even traits such as flower color and leaf resistance may be correlated due to pleiotropy or linkage. For example, flower color polymorphism in *Ipomoea purpurea* correlated with differences in leaf herbivore resistance (Simms and Bucher 1996), although such differences may not affect damage in the field

(Fineblum and Rausher 1997). In *Raphanis sativus*, flower color morph is correlated with lower levels of indole glucosinolates in leaves, and preference and performance of a variety of leaf herbivores (Irwin et al. 2003). Such differential effects of flower color on leaf herbivory may explain why pollinator preference alone does not predict microevolution of floral color morphs (Irwin and Strauss 2005). Furthermore, alkaloid concentrations are correlated in leaves and corollas of naturally growing *Gelsemium sempervirens* (Irwin and Adler 2006), although these correlations may be due to genetic or environmental variation. The expression of nicotine and related alkaloids in nectar and leaves is phenotypically correlated across individual *Nicotiana tabacum* plants (Adler et al. 2006) and is also correlated across *Nicotiana* species (L. S. A., M. Gittinger, G. Morse, and M. Wink, unpublished data). Although not the subject of this chapter, related literature addresses the causes and consequences of toxic ripe fruit for fruit dispersers (e.g., Cipollini and Levey 1997; Cipollini 2000; Tewksbury and Nabhan 2001). Toxicity in ripe fruit may be correlated across species with toxicity of leaf defenses (Ehrlen and Eriksson 1993), providing another example where the evolution of attractive rewards (ripe fruit) may be constrained by expression of defenses in other tissues. Thus, a growing number of studies demonstrate that selection by pollinators on flower color or floral secondary compounds could drive correlated evolution of leaf traits, and selection by leaf herbivores on resistance could alter the evolution of flower color or defense (Lande and Arnold 1983). However, much work remains to elucidate the genetic basis of correlated traits across plant tissues to determine the generality of these results.

Leaf damage may alter floral traits. Optimal defense theory predicts that flowers will be constitutively defended due to their high reproductive value (McKey 1974; Rhoades and Cates 1976), and this prediction is supported by high levels of constitutive resistance in *Pastinaca sativa* flowers compared to leaves and roots (Zangerl and Rutledge 1996). However, recent studies have found that flower defense is also inducible. For example, leaf damage induced higher petal glucosinolate concentrations in anthocyanin-containing color morphs of *Raphanus sativus* (Strauss et al. 2004). In *N. attenuata*, leaf damage increased nicotine concentration in flowers (Euler and Baldwin 1996) and fruits (Baldwin and Karb 1995) and increased resistance to floral and fruit herbivory in the field (McCall and Karban 2006). Leaf damage by *Manduca sexta* induced higher levels of nectar nicotine in *N. tabacum* (Adler et al. 2006). Thus, leaf damage can affect floral traits, which may alter interactions with both pollinators and floral antagonists.

Herbivores and Pollinators May Not Be Independent

Plant interactions with herbivores and pollinators are often studied as separate and independent. However, in many systems herbivores and pollinators are the same species inter-

acting with plants at different points in their life cycle. In some cases, pollinators oviposit into flowers or fruits that are subsequently consumed by larval seed predators; these systems can be highly obligate, such as the yucca plant–yucca moth (Pellmyr 2003) and fig plant–fig wasp interactions (Bronstein 1988; Kjellberg et al. 2001), or somewhat facultative, such as interactions between *Silene* and *Hadena* moths (Pettersson 1992; Wolfe 2002). In other cases, pollinators may oviposit leaf-feeding larvae whose success is less linked with pollinator behavior. In any case, if adults prefer plants with attractive rewards such as high nectar volumes (e.g., Real and Rathcke 1991; Hodges 1995), then attractive traits may be under conflicting selection to attract pollinators but minimize the linked cost of herbivory. I review some examples here; more complete coverage is provided by Adler and Bronstein (2004).

Members of the family Sphingidae (the hawkmoths) provide perhaps the best examples of herbivorous larvae that specialize on the same plants pollinated by adults (reviewed in Adler and Bronstein 2004). Such herbivory may represent a significant cost to plants. For example, an individual *Manduca sexta* larva can defoliate its host by the time it pupates (McFadden 1968). Among other Lepidoptera, *Pieris rapae* (Pieridae) is an efficient pollinator of *Raphanus raphanistrum* (Conner et al. 1995), and larval *P. rapae* are specialists on crucifers including this species (e.g., Agrawal 1999). Finally, several moths and butterflies that are generalist nectar-feeders as adults and generalist herbivores as larvae may incorporate certain plant species in their diets at both life-history stages; examples include *Heliothis virescens* and *Helicoverpa armigera* (Cunningham et al. 1998; De Moraes et al. 2001). This is not intended as an exhaustive list, but rather as examples that demonstrate the potential for trade-offs between attracting pollinators and experiencing increased levels of herbivory from offspring.

Only two experiments have tested the hypothesis that floral attractants could increase levels of oviposition by leaf herbivores. Adding supplemental nectar to *Datura stramonium* flowers increased the number of *M. sexta* eggs oviposited on leaves (Adler and Bronstein 2004). *Manduca sexta* is a voracious herbivore of *D. stramonium*, whose adults are also common nectar-feeding pollinators on the same plants (L. S. A., personal observations). Similarly, increasing the quality of nectar with supplemental arginine, a naturally occurring amino acid essential for egg maturation, increased *M. sexta* leaf oviposition on *N. tabacum* (A. J. Lentz and L. S. A., unpublished). Both of these studies were conducted in cages stocked with artificially high levels of *M. sexta* moths, and both removed eggs before hatching and so could not quantify the costs of herbivory. Furthermore, in these systems there was no benefit of supplemental nectar amount or quality on plant female reproduction, presumably because both *D. stramonium* and *N. tabacum* are highly selfing (Goodspeed 1954; Motten and Antonovics 1992). However, these studies represent the first steps in demonstrating that floral rewards, by attracting pollinators, may also increase leaf herbivory. Further work is needed to

demonstrate whether such trade-offs occur in the field under natural insect densities, and to quantify the benefits and costs of floral traits in the context of attracting both pollinators and their herbivorous offspring.

Abiotic Factors and Geographic Variation

Selection pressures do not remain constant over time or space. Variation in the abiotic and biotic environment can alter both the expression of phenotypes and the relative importance of different selective agents. There is ample evidence that abiotic conditions mediate attractive and defensive phenotypes (e.g., Gershenzon 1984; Mattson and Haack 1987; Wyatt et al. 1992; Galen 1999b; Carroll et al. 2001; Gardener and Gillman 2001), and that selection is spatially, temporally, and environmentally heterogeneous (Boag and Grant 1981; Kalisz 1986; Stratton 1992; Dudley 1996; Stratton and Bennington 1998). However, few empirical studies have examined how selection by multiple biotic agents changes under different abiotic conditions (but see Galen 1999a; Galen and Cuba 2001; Ehrlen et al. 2002).

Although the influence of abiotic factors on selection by biotic agents has long been recognized in studies of the evolution of plant defenses (e.g., Bryant et al. 1983; Coley et al. 1985), the role of abiotic factors has only recently been studied for the evolution of floral diversity (Galen 1999b; Elle 2004), and there are few empirical tests. In two such natural experiments, pollinator selection on flower morphology changed between wet and dry years (Maad 2000; Maad and Alexandersson 2004) and across an altitude-temperature gradient (Totland 2001). Furthermore, expression of traits involved in pollinator attraction, such as flower color, may be linked with traits involved in drought tolerance (Schemske and Bierzychudek 2001), suggesting that both abiotic and biotic factors may simultaneously influence the selective advantage of plant traits. Abiotic conditions may also affect the relative significance of selection by herbivores and pollinators. In particular, resources such as water or nutrients may determine whether a plant is pollen limited and therefore the importance of pollinator attraction (Haig and Westoby 1988; Zimmerman and Pyke 1988). Reductions in pollinator visitation may not affect fitness in harsh conditions, where limited resources constrain fecundity, but may significantly reduce fitness in favorable conditions (e.g., Campbell and Halama 1993; Corbet 1998). In harsher conditions, pollinator-mediated selection may be reduced while herbivore-mediated selection remains constant or increases. Therefore, the relative importance of herbivore defense and pollinator attraction may change in different environmental contexts.

Community context may also change the pattern of selection on attractive or defensive traits. For example, the presence of an alternate pollinator changed the outcome of the interaction between a plant and pollinating seed predator from positive to negative for the plant (Thompson and Cunningham 2002). The effect of low-efficiency pollinators

on plant fitness in *Campanula americana* varied from neutral to negative, depending on the abundance of high-efficiency pollinators (Lau and Galloway 2004). The presence of another plant species that competes for pollination services can also change the shape of selection on floral traits in a focal plant species (Caruso 2000, 2001). These examples demonstrate the importance of community context in shaping selection on attractive and defensive phenotypes. It is likely that community composition plays a large role in determining the magnitude and direction of interactions between plants, herbivores, and pollinators in many systems.

Future Directions

The goal of this review was to gather and synthesize a wide range of studies demonstrating the potential for herbivores to select on floral attraction, and for pollinators to select on plant resistance. Many of these studies are quite recent, demonstrating both a historical lack of attention to the potential for multispecies selection on plant traits, and a recent excitement to pursue such questions in greater depth. While these studies represent a large and growing body of work, there are clear gaps in our understanding of these interactions that should be the focus of future research.

While the traits responsible for resistance to leaf herbivores have been extensively studied, we know very little about the traits responsible for resistance to other herbivores, such as floral antagonists and root herbivores. For example, although nectar robbers can reduce plant fitness as much as leaf herbivores (Juenger and Bergelson 1997; Irwin and Brody 2000), only a handful of studies have attempted to determine what traits confer resistance to nectar robbing. Observational and manipulative studies are needed to elucidate whether the same or correlated traits are involved in attracting pollinators and deterring floral antagonists (e.g., Irwin et al. 2004).

Traits must be experimentally manipulated to isolate their effect on species interactions. Historically, mechanical (e.g., constraining floral tube shape [Galen and Cuba 2001]) or chemical (e.g., addition of hormones to induce changes [Thaler 1999]) manipulations have been used. However, the increasing feasibility of isolating and transforming or knocking out specific loci allows a greater range of manipulations and understanding of the mechanistic basis of trait expression (e.g., Kessler et al. 2004). The use of genetic modification to manipulate traits provides another powerful tool to address how such traits evolve in natural contexts.

Understanding the genetic correlations between traits expressed across tissues, such as secondary compounds in leaves and nectar, or pigmentation in flowers and vegetative tissue (e.g., Armbruster 2002), is of fundamental importance for predicting how leaf herbivores could exert correlated selection on floral traits, or how pollinators could drive the evolution of resistance traits in leaves. Furthermore, the

heritability of some basic traits is poorly understood. Although nectar production and composition are critical for pollinator attraction in many systems (Dafni 1992; Pellmyr 2002) and may also attract herbivores and natural enemies, as of 2004 only seven published studies had examined the heritability of nectar traits in wild plant species (Mitchell 2004). Even less is known about the heritability of extrafloral nectar traits (but see Rudgers 2004).

One of the fundamental goals of evolutionary ecology is to understand how traits evolve in the context of their environments, but there are currently no studies that quantify the extent of selection by herbivores and pollinators on resistance or attractive traits. Determining the role of selection by herbivores or pollinators on the evolution of plant traits requires manipulating or removing the putative agent of selection and measuring changes in the pattern of selection on the traits of concern. Such studies have shown that pollinators can select on floral traits (e.g., Campbell et al. 1991; Galen 1996; Jones and Reithel 2001) and herbivores can select on plant defensive traits (e.g., Mauricio and Rausher 1997). However, as this review has shown, numerous traits may influence both attraction and defense. Little is known about the *relative* importance of selection by mutualists and antagonists on attractive and defensive traits (but see Gomez and Zamora 2000; Herrera 2000; Herrera et al. 2002). This question could be addressed by manipulating herbivores and pollinators and measuring resultant changes in the magnitude or direction of selection on both floral and defensive traits, or by examining selection in multiple populations that vary in herbivory or pollination frequency. Such studies would be intensive due to the sample sizes required to detect changes in selection (Kingsolver et al. 2001) but would be feasible in some systems. Good candidate systems would be *Brassica* and *Raphanus* species, in which the genetic basis of resistance traits is well understood (Strauss et al. 1999; Irwin et al. 2003), resistance traits reduce herbivore preference and performance (Giamoustaris and Mithen 1995; Irwin et al. 2003), leaf herbivory reduces pollinator attraction (Lehtila and Strauss 1997), pollinators are necessary for reproduction (Strauss et al. 1996), and flower traits are correlated with leaf defenses (Irwin et al. 2003; Strauss et al. 2004). Alternatively, on a macroevolutionary scale one could look for evolutionary changes in herbivore resistance that correlate with changes in pollinator mode, or vice versa, and test predictions about the conditions under which such evolutionary correlations might occur. These approaches would help to assess the relative role of pollinators and herbivores in altering the evolution of attraction and defense across microevolutionary and macroevolutionary time scales.

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