

# ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF MULTISPECIES PLANT-ANIMAL INTERACTIONS

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■ **Abstract** Ecologists and evolutionary biologists are broadly interested in how the interactions among organisms influence their abundance, distribution, phenotypes, and genotypic composition. Recently, we have seen a growing appreciation of how multispecies interactions can act synergistically or antagonistically to alter the ecological and evolutionary outcomes of interactions in ways that differ fundamentally from outcomes predicted by pairwise interactions. Here, we review the evidence for criteria identified to detect community-based, diffuse coevolution. These criteria include (a) the presence of genetic correlations between traits involved in multiple interactions, (b) interactions with one species that alter the likelihood or intensity of interactions with other species, and (c) nonadditive combined effects of multiple interactors. In addition, we review the evidence that multispecies interactions have demographic consequences for populations, as well as evolutionary consequences. Finally, we explore the experimental and analytical techniques, and their limitations, used in the study of multispecies interactions. Throughout, we discuss areas in particular need of future research.

## INTRODUCTION

A major goal in ecology and evolutionary biology is to understand how the interactions among organisms influence their abundance, phenotypes, and genotypes. Although the complexity of interactions in natural systems has been acknowledged (e.g., Billick & Case 1994, Juenger & Bergelson 1998, Paine 1992, Polis & Strong 1996, Wootton 1993), studies in terrestrial plant-animal interactions have classically focused on direct, pairwise interactions. More recently, however, an appreciation has developed of how multispecies interactions significantly alter both the ecological and evolutionary outcomes of interactions in ways that could not be predicted from an understanding of pairwise interactions alone (Miller & Travis 1996, Pilson 1996, Strauss 1991, Thompson 1999). The community context of interactions, primarily in terrestrial plant-animal systems, is the focus of this paper,

and our goal is to review and highlight common themes among disparate studies of multispecies interactions. Because this area is so large, we focus this review almost solely on the responses of plants to community membership; however, the same kinds of interactions and selective effects also occur for the animals participating in these interactions.

Plants rarely interact with a single mutualistic or antagonistic species. Rather, sessile plants must integrate interactions across a suite of different mutualists and antagonists, usually simultaneously. These visitors are taxonomically diverse, use many different parts of a plant, and usually vary in their impacts on plant fitness along a continuum from positive to negative, direct to indirect. For example, when plants are attacked by enemies, a cascade of responses typically ensues. Common plant reactions to damage include altered allocation to root:shoot biomass, short-term increases in photosynthetic rate, and the induction of costly structural and chemical defenses in plant tissues. Changes in allocation to reproductive structures such as floral size and rewards after damage have been shown to alter relationships with pollinators (see section below). Moreover, induced responses are often systemic and may influence relationships with pathogens, enemies of herbivores, and other community members. Understanding how plants and animals interact and evolve in this community context is key to understanding trait evolution. Below, we consider the evidence for criteria that create conditions under which diffuse, community-dependent evolution or selection could occur. In addition, we review the evidence that these multispecies interactions have ecological demographic consequences for plant populations, as well as evolutionary consequences. Throughout, we emphasize the areas that we think offer the most promising prospects for future research.

## PAIRWISE VERSUS DIFFUSE EVOLUTION

The idea that communities exert selective pressures that differ fundamentally from those imposed by multiple, pairwise combinations of species has been discussed for many years, and the term “diffuse coevolution” was introduced by Janzen (1980) in his seminal note *When Is It Coevolution?* In recent prominent papers, several authors have outlined criteria to evaluate whether evolution is diffuse (determined by interactions with many species), as opposed to pairwise (reflecting the independent interactions between pairs of species, even multiple pairs) (e.g., Hougen-Eitzman & Rausher 1994, Stinchcombe & Rausher 2002, Iwao & Rausher 1997).

In pairwise evolution, traits involved in one set of interactions evolve independently of traits involved in other interactions. The evolutionary dynamics of the two interacting species are independent of the presence or actions of other community members. For evolution to be driven by some emergent property of multispecies communities, effects of interactors should be nonadditive; that is, one could not predict the selective pressures a focal species would experience simply

from knowing the selective effects of each interacting species alone. However, both additive and nonadditive effects of multiple species may lead to diffuse selection. The following criteria have been proposed to determine whether selection is diffuse. These criteria were originally proposed for herbivores only and were presented as criteria for pairwise evolution that, if violated, would provide evidence for diffuse evolution. They are paraphrased from the original papers to reflect criteria for broad communities and to reflect diffuse selection (Hougen-Eitzman & Rausher 1994, Iwao & Rausher 1997, Stinchcombe & Rausher 2002).

1. Traits important to interactions with multiple species are genetically correlated with one another; that is, selection on one trait will influence the value of traits important in other interactions. We add to this criterion the variant that there may be conflicting selection on the same trait exerted by multiple interactors.
2. The presence or absence of one community member mediates interactions with others. For example, attack by one species alters the likelihood or intensity of interactions with, or selection by, other community members.
3. The effects of multiple interactors on plant fitness are not additive. Thus, the effect of species in combination on the fitness of a focal species are not just the sum of the effects of each species separately. In considering such effects, it may be conceptually useful to divide effects of the interactors on fitness into (a) the cumulative costs (or benefits) of response to the interactors and (b) the effects of the interactors themselves (Miller & Travis 1996). As stated, this criterion addresses ecological impacts of multiple species more than evolutionary ones, because to show diffuse selection, one must focus on the nonadditive effects of species on the relationship between trait(s) and fitness, not fitness alone (see Inouye & Stinchcombe 2001, Strauss et al. 2004 for more discussion.)

What evidence do we have that bears on these criteria? Although a number of studies address criterion 2, surprisingly few studies have addressed whether genetic correlations exist among traits important in multispecies plant-animal interactions (criterion 1) and whether the impacts of multiple interactors on plants are nonadditive (criterion 3, especially for multispecies mutualisms). Here, we review evidence for each criterion from a diverse suite of multispecies plant-animal interactions.

### Criterion 1: Genetic Correlations Among Traits

When traits important to interactions with multiple species are genetically correlated with one another, multiple interactors can affect the evolution of single traits. The nature of the correlation, as well as the nature of interactions with multiple species, will promote or de-emphasize the community context of such evolution. In addition, traits that have effects on multiple interactions will be shaped by the combined effects of community members.

Consider a simple scenario of a pair of genetically correlated plant traits, X1 and X2, in which increased values of X1 attract one insect species and increased values of X2 attract a different insect species. If both insects are mutualists or if both are antagonists, a positive genetic correlation between X1 and X2 could speed the rate of fixation of alleles that influence these traits. In this case, both agents drive correlated traits in the same direction, even in years when one agent is less abundant or less important in determining plant fitness. The community context will affect the speed, but not the outcome, of evolutionary change.

On the other hand, if the two insect species have opposing effects on plant fitness—for example, one is a pollinator and the other is a seed predator—then a positive genetic correlation between X1 and X2 is likely to result in selection that fluctuates, and may even change sign, with changes in insect abundance and interaction strength. In this case, fluctuating selection may prevent the fixation of alleles that optimize values of traits X1 and X2.

A negative genetic correlation between these traits would have similar effects. When both insects are antagonists (or both are mutualists), we expect fluctuating selection. However, if the two insect species have opposing effects on plant fitness, we expect fixation of alleles in these traits because both agents are driving traits in the same direction because of their correlated responses. In these scenarios, community context and the frequency and intensity of fitness impacts of multiple community members become critical to understanding trait evolution. Interactions in the field are notoriously variable in strength because species composition and abundance varies from year to year, and the strength of the interactions may be modified by the presence or absence of other community members, for example, another pollinator or seed predator (Thompson 1994) or abiotic conditions (Galen 1999).

**HERBIVORE-HERBIVORE INTERACTIONS** In a recent review, Rausher (1996) stated that most genetic correlations between resistance to different herbivores were either zero or positive. A correlation of zero means that defense traits are evolving in response to independent pairwise interactions (barring the existence of phenomena in criteria 2 and 3). However, Berenbaum et al. (1986) showed negative genetic correlations between the amounts of different secondary compounds in *Pastinaca sativa* (Apiaceae) and, thus, documented constraints on the evolution of resistance to different herbivores because compounds were differentially effective at deterring different herbivore species. Since the review by Rausher (1996), a few more cases of negative genetic correlations between attack by different herbivores have been documented (Juenger & Bergelson 1998, Mitchell-Olds et al. 1996, Stinchcombe & Rausher 2001), along with other studies that show positive or no genetic correlations (Tiffin & Rausher 1999).

**TRAITS INVOLVED IN VARIOUS MULTISPECIES INTERACTIONS** Remarkably few studies have undertaken examinations of genetic correlations between traits important in diverse, simultaneous interactions across a wide range of taxa and

interactions. Siemens & Mitchell-Olds (1998) found a negative genetic correlation between resistance to the fungal pathogen *Peronospora parasitica* and plant-growth rate in *Brassica rapa* (Brassicaceae), a result that suggests the possibility of a disease resistance/plant competition tradeoff. Similarly, *Diplacus aurantiacus* (Scrophulariaceae) and *Pastinaca sativa* exhibit negative genetic correlations between the production of secondary plant metabolites that possess documented antiherbivore functions and plant growth rate (Berenbaum et al. 1986, Han & Lincoln 1995). For *Diplacus aurantiacus*, the production of 1 mg of resin content comes at a cost of 25 mg of dry-shoot biomass growth (Han & Lincoln 1995). Again, this result supports the possibility that better-defended plants may be poorer competitors for light and resources, but such growth/defense tradeoffs (Coley et al. 1985) remain to be documented in these systems. A phenomenon that might work against such a tradeoff is the possibility that increased levels of secondary compounds may also serve as allelochemicals that suppress competitors (Siemens et al. 2002). This suppression may offset the costs of production of these compounds in terms of growth rate and, thus, may not result in a defense/competition tradeoff.

To our knowledge, no studies to date document a negative genetic correlation between separate attraction and defense traits in plants, although Strauss et al. (2004) come close. After crossing plants into similar genetic background and using only greenhouse-grown plants to control for parental environment, they found a significant correlation between petal pigment, which is heritable, and foliar glucosinolate content, which serves as a defense against herbivores and also has a heritable basis (Strauss et al. 2004). Anthocyanin-dominant purple and bronze morphs of *Raphanus sativus* (wild radish; Brassicaceae) had greater induction of foliar glucosinolates than did anthocyanin-recessive yellow and white morphs. In addition, field evidence shows that pollinators prefer yellow-flowered plants (see also Stanton 1987), the least-defended genotype. Herbivores, on the other hand, generally had better performance on yellow and white genotypes and, thus, should act to select against anthocyanin-recessive morphs in the field (Irwin et al. 2003). As a result of the linked expression of these traits, herbivores may affect petal-color traits important to pollinators, and pollinators may drive variation in defense traits by favoring the least-defended, yellow genotype. Given the large amount of work that has focused on plant-animal interactions, surprisingly few studies have investigated genetic correlations between traits involved in interactions with diverse community members.

**CONFLICTING SELECTION PRESSURES ON THE SAME TRAIT** Opposing selection by antagonistic and mutualistic community members may be particularly common for attractive characters, such as flowers, because mutualists and antagonists alike can use these conspicuous traits to locate plants. Such examples might be thought of as ecological pleiotropy, wherein the same trait affects multiple interactions. In some cases, community members can act upon the same trait in opposing directions, which makes fitness effects of the trait in different ecological contexts negatively

genetically correlated. Community-based selection is then likely to influence the evolution of ecologically pleiotropic traits in fluctuating environments. How the community context influences selection will depend, in part, on whether community composition covaries with factors that increase or decrease the average performance of a focal species and on whether selection is hard or soft (Futuyma 1986).

Some well-known instances of conflicting selection pressures imposed by different community members on the same traits include pollinators versus seed predators (e.g., Brody 1992) and pollinators versus florivores/nectar thieves (e.g., Galen & Cuba 2001, Gómez 2003, Herrera et al. 2002). Floral traits often reflect an adaptive compromise between relationships with mutualistic pollinators and relationships with antagonists (Brody 1992, Galen & Cuba 2001). Different plant parts have typically been ascribed to serve in each function—sepals and the ovary wall protect the ovary and developing seed (Grant 1950), whereas the corolla or modified sepals serve in pollinator attraction and efficacy. However, defense and attraction functions may not be as easily partitioned as initially thought. Petals are defended against herbivores (Euler & Baldwin 1996, Strauss et al. 2004), and the degree to which nectar and pollen reward chemistry are independent of petal and leaf chemistry is unclear (Adler 2000). In *Hypericum calycinum* (Hypericaceae) flowers, the same ultraviolet pigments play a defensive role in the stamens and ovaries and an attractive role in the petals (Gronquist et al. 2001). In the *Dalechampia* clade (Euphorbiaceae), resins involved in chemical defense against herbivores and microbes have secondarily assumed a role in pollinator attraction and reward, and bracts serving to attract pollinators have been co-opted as a defense against flower-feeding herbivores (Armbruster 1997).

Galen has done some of the most complete work on how the effects of extremely diverse selective agents affect trait evolution in plants (reviewed in Galen 1999). In this case, different agents are acting in opposing directions on the same corolla flare/corolla tube-length traits, which are positively genetically correlated. Flowers of the alpine sky pilot, *Polemonium viscosum* (Polemoniaceae), that have smaller, narrow corollas experience lower risk of predation on floral parts from nectar-thieving ants than do larger, more flared flowers. However, as documented by experimental manipulations and observations in the field, narrow-tube forms, although better defended from ants, receive 47% fewer pollen grains and set 62% fewer seeds than do flared corollas. This difference in reproductive success reflects the foraging behavior of bumblebee pollinators that also seek nectar rewards. In this case, both mutualist pollinators and antagonist nectar thieves forage for the same nectar reward and use flower shape and size as a cue (Galen 1999). Moreover, in high-elevation populations, water stress favors smaller corollas that reduce water loss from the plant. Thus, the benefits of bee pollination counter costs of predation by ants and water loss in flared corolla morphs.

Several other cases are known in which herbivores and pollinators act on the same floral traits (Brody 1992, Ehrlén et al. 2002). Scape length in *Primula farinosa* (Primulaceae) appears to be under opposing selection from seed predators

and pollinators (Ehrlén et al. 2002). Similarly, tall *Erysimum mediohispanicum* (Brassicaceae) plants exposed to browsers are selected against because of grazing, whereas tall plants inside ungulate exclosures are favored by pollinators (Gómez 2003). In a different correlative study across 20 species of composites (with three additional within-species comparisons), increasing capitulum size was associated with increasing incidence of infestation from bud predators and was not correlated with other variables, a result that suggests that capitulum size may be determined primarily from opposing selection from pollinators and bud predators (Fenner et al. 2002).

Opposing selection on the same trait can also be seen in tradeoffs between resistance to generalist and specialist herbivores: specialists often use volatiles to locate hosts and often have the ability to detoxify, sequester, or excrete secondary compounds. In contrast, generalist herbivores are often deterred by the presence of high concentrations of these same compounds. Thus, plants that are well defended against generalists are often consumed by specialists (Gatehouse 2002). Taken together, these examples suggest many cases in which the same trait comes under opposing selection from multiple community members.

## **Criterion 2: Interactions with one Species Affect the Likelihood or Intensity of Interactions with Other Species**

Community context can affect the likelihood or intensity of interactions among community members and can have important ecological effects on the population size of interactors as well as important evolutionary effects if they change patterns of selection on traits. Patterns of plant use, and potential patterns of selection on plants, may be influenced by interactions through at least two common pathways: density-mediated effects and trait-mediated effects (for a review, see Wootton 2002). Density-mediated effects arise when plant-animal interactions are altered through changes in population density of community members. For example, herbivores may alter plant–seed disperser interactions through changes in seed density. Alternatively, trait-mediated effects arise when interactions with one species cause a change in trait value that subsequently affects interactions with a third species; for example, herbivores may change plant–pollinator interactions through changes in the quality of flowers produced. Shifts in ecological interactions may translate into altered selective landscapes. The presence of spider predators can cause grasshoppers to shift from eating primarily grasses to primarily forbs (Schmitz 1998) and may therefore have impacts not only on forb and grass abundance but also on the defensive traits of these co-occurring species.

One theme running through all of the studies described below is that trait-mediated effects are particularly common. Trait-mediated effects are pervasive properties of interacting species. Their effects may be nonadditive and difficult to predict in isolation (Wootton 1993). In general, most organisms have immune or defensive systems that respond dynamically and plastically to attack from pathogenic or trophic organisms. Such responses are likely omnipresent (see Table 1 for

**TABLE 1** Scenarios under which plant interactions with one species could affect the likelihood or intensity of plant interactions with others<sup>a</sup>

Scenario	Type of interaction	Example of potential mechanism involved	Exemplar reference
Antagonist → antagonist	Herbivore → herbivore	Induction of defensive trait	Karban & Baldwin 1997
	Pathogen → herbivore	SAR pathway	Rojo et al. 2003
	Herbivore → seed predator	Change in flowering phenology	Juenger & Bergelson 1998
Mutualist → mutualist <sup>b</sup>	Pollinator → pollinator	Pollinator scent marks	Stout & Goulson 2001
	Ant → ant	Competition for rewards	Palmer et al. 2003
	Granivore → granivore	Change in vegetation structure	Valone et al. 1994
	Pollinator → granivore	Change in fruit/seed abundance	— <sup>c</sup>
	Granivore → pollinator	Change in plant demography	—
	Nectar robber → pollinator	Change in nectar availability	Irwin & Brody 2000
	Mycorrhizae → pollinator/ fruit disperser	Change in nectar or fruit quality	—
	Endophytic fungi → enemies of herbivores	Change in plant quality	Omacini et al. 2001
	Endophyte → granivore	Change in seed quality	Madej & Clay 1991
Antagonist → mutualist <sup>b</sup>	Herbivore → pollinator	Change in floral traits	Mothershead & Marquis 2000
	Herbivore → granivore	Change in vegetation structure	Smit et al. 2001
	Herbivore → mycorrhizae	Change in plant-resource status	Eom et al. 2001
Mutualist <sup>b</sup> → antagonist	Pollinator → seed predator	Change in fruit/seed rewards	Herrera 2000
	Granivore → herbivore	Change in seedling demography	—
	Endophyte → herbivore	Induction of defensive trait	Clay et al. 1993
	Mycorrhizae → herbivore	Change in plant quality	Gange et al. 2002

<sup>a</sup>This list should be considered as a starting point for the types of multispecies interactions that could occur and is by no means exhaustive. The strength and outcome of many of these multispecies interactions are conditional on the organisms involved and on the environmental conditions in which they occur (see text).

<sup>b</sup>Mutualists can vary in the strength of their positive effects on plants depending on community context (reviewed in Stanton 2003). We are lumping granivores into “mutualists” here because sometimes granivores can increase seedling germination by dispersing or caching seeds; however, we fully realize that costs are associated with granivory as well, and sometimes the costs can outweigh the benefits. The same logic applies to nectar robbers and endophytes.

<sup>c</sup>Dashes indicate that we were unable to find a study that conclusively demonstrated the proposed interaction. These types of interactions are in need of further empirical attention.



different categories of interactions and an exemplar mechanism and citation). Below, we review the literature for interactions that have not received much prior attention and suggest review articles for other topics that have been recently reviewed.

**HERBIVORE-HERBIVORE/PATHOGEN INTERACTIONS** Defenses induced by pathogen or herbivore attack in plants fit well within the trait-mediated paradigm. Karban & Baldwin (1997) document more than 24 cases in which attack by one herbivore results in altered levels of leaf damage by, attractiveness to, or mortality of, another subsequently interacting herbivore species that fed on the same plant. These examples were drawn solely from the agricultural literature, but numerous other examples suggest that these effects are ubiquitous in native systems as well (e.g., 13 examples from natural systems in Hougén-Eitzman & Rausher 1994).

In addition, a growing body of literature discusses cross-talk between induction from pathogens that cause upregulation of the salicylate (SA)-based systemic acquired resistance (SAR) and ethylene (E) pathways in plants and the jasmonate-based (JA-based) induced-response (IR) pathway stimulated by insect attack. In some cases, these pathways appear to compete with one another, such that upregulation of the SA pathway caused by disease makes plants more susceptible to insect attack (and less susceptible to disease), whereas induction of JA by insects has the reverse effect (Rojo et al. 2003, Thaler et al. 2002).

**MUTUALIST-MUTUALIST INTERACTIONS** Just as herbivore feeding can influence plant resistance to subsequent enemy attack, patterns of host-plant use by one mutualist may alter subsequent plant-mutualist interactions. For example, many pollinators leave attractant and repellent scent marks that affect subsequent floral visitation (Goulson et al. 2000, Guirfa 1993). Stout & Goulson (2001) found that scent marking by *Bombus lapidarius* on the flowers of *Melilotus officinalis* (Fabaceae) deterred conspecific and heterospecific (*Apis mellifera*) floral visitors over a 40-minute period. Similarly, pollinator visitation may induce flower-color change in many plant species and have subsequent effects on floral visitation (Gori 1983). Hummingbird pollinators of *Malvaviscus arboreus* var. *mexicanus* (Malvaceae) avoid flowers that have been nectar robbed by orchard orioles in 97% of their visits because of a color change associated with damaged, older flowers (Gass & Montgomerie 1981). Conversely, floral visitation to some plant species stimulates nectar production (e.g., Gill 1988), which may increase total visitation to plants by the pollinator assemblage.

When mutualists share the same resource, competition for access to host rewards may be widespread and important in the patterns of host use by multiple species (recently reviewed in Palmer et al. 2003). Shifts in the community composition of mutualists may, in turn, exert selection on plant traits. For example, a strong dominance hierarchy among four ant species for a limiting host tree, *Acacia drepanolobium* (Mimosaceae), in Kenya affects spatial patterns of host-tree use by subordinate ant species (Palmer 2003). Africanized honey bees in French Guiana

indirectly determine the abundance of native pollinators (and potentially native pollinator visitation to flowers) through exploitative competition for floral rewards (Roubik 1978, 1980). Inouye (1978) experimentally removed the bumblebee *Bombus appositus* from the flowers of its preferred host species, *Delphinium barbeyi* (Ranunculaceae), and found increased visitation by another bumblebee species, *B. flavifrons*. Conversely, removal of *B. flavifrons* from *Aconitum columbianum* (Ranunculaceae) resulted in increased visitation by *B. appositus*. These results suggest that resource utilization by one species influenced the visitation patterns of the other species. In the case of plant-pollinator/nectar-robber interactions, visits by the nectar-robbing bumblebee, *Bombus occidentalis*, decrease subsequent visitation by hummingbird pollinators (Irwin & Brody 1998) because of reduced nectar availability. In all of these studies, access to rewards or modification of rewards results in alterations in host use within multispecies mutualisms.

Interactions among other mutualists, such as seed dispersers and harvesters, may also be driven by a combination of direct and indirect effects via changes in vegetation, resource abundance, or resource distribution. For example, in an impressive three-way factorial design, Longland et al. (2001) excluded scatter-hoarder and larder-hoarder rodents and ant seed dispersers and consumers of Indian ricegrass (*Oryzopsis hymenoides* [Poaceae]). They found significantly more ant larders in plots with rodents excluded than in plots with rodents present, which suggests that rodent activity affected ant activity.

**HERBIVORE-POLLINATOR INTERACTIONS** Recently, the role of trait-mediated effects of herbivore damage on the numbers and behaviors of mutualist pollinators has received experimental attention. Distinguishing among the different kinds of herbivores (i.e., foliar versus floral herbivore) is useful when these interactions are considered. Foliar herbivory has been shown to diminish the amounts or quality of floral rewards (e.g., Frazee & Marquis 1994, Lehtilä & Strauss 1999, Mutikainen & Delph 1996) and flower size (e.g., Cresswell et al. 2001, Strauss et al. 1996) and cause induction of chemicals in floral or reward chemistry (Euler & Baldwin 1996, Strauss et al. 2004). Although these studies document changes in postdamage floral traits, only a few studies show the impacts of foliar damage on subsequent pollinator visitation. Generally, pollinators tend to visit damaged plants less frequently or for shorter durations (Hambäck 2001, Lehtilä & Strauss 1997, Mothershead & Marquis 2000, Strauss et al. 1996), but sometimes damage has no effects on visitation patterns (Hambäck 2001, Strauss et al. 2001); in one case, herbivory by wireworms caused an increase in pollination in *Sinapis arvensis* (Brassicaceae) (Poveda et al. 2003). Because of self-incompatibility, stigmatic clogging, and geitonogamy, to name just a few factors, translating pollinator-foraging behavior into impacts on plant fitness can be difficult. Even fewer studies examine the effects of foliar herbivory via pollinators all the way to impacts on plant fitness (but see Mothershead & Marquis 2000, Strauss et al. 2001).

In contrast, a bit more attention has been paid to the effects of florivory on both pollination and plant reproduction. Again, florivory generally reduces subsequent

pollinator visitation to damaged plants (e.g., Galen 1999, Krupnick et al. 1999, and see references in Table 2) through a number of different mechanisms, such as decreasing flower number, increasing floral asymmetry, and decreasing petal size and floral conspicuousness (e.g., Alados et al. 2002).

**HERBIVORE-SEED PREDATOR/DISPERSER INTERACTIONS** Herbivory not only affects plant-pollinator interactions but also plant-seed predator interactions. In some cases, these effects may be caused by changes in the traits of plants after herbivory. For example, in the monocarpic herb *Ipomopsis aggregata* (Polemoniaceae), herbivory of the flowering stalk by mule deer reduces oviposition by the predispersal seed-predator fly *Hylemya* spp. (Freeman et al. 2003, Juenger & Bergelson 1998). One likely mechanism that explains reduced seed-predator oviposition on browsed plants is that herbivory induces a delay in flowering phenology, which results in a mismatch between peak-flower and seed-predator abundance (Brody 1997, Freeman et al. 2003), although other mechanisms, such as changes in floral display size or plant or fruit chemistry, cannot be ruled out (Juenger & Bergelson 1998).

Herbivory can also affect the activity of granivores. For example, exclusion of mammalian herbivores from pine and oak woodland communities increased granivory by wood mice (*Apodemus sylvaticus*) and field voles (*Microtus agrestis*), likely because of herbivore-induced changes in vegetation structure (Smit et al. 2001). Reversing the interaction, postdispersal seed predators could affect seedling herbivory in populations where seedling herbivory is density dependent. Indirect evidence suggests that the activity of seedling predators (meadow voles, *Microtus pennsylvanicus*) and seed predators (white-footed mice, *Peromyscus leucopus*) in North American old fields is negatively correlated. Experimental manipulation of seedling predators affected the activity of seed predators (Ostfeld et al. 1997), and the opposite pattern may also hold in cases where the activity of seedling predators is dependent on seedling density, although such a scenario was not experimentally tested to our knowledge.

**POLLINATOR-SEED PREDATOR INTERACTIONS** Whereas herbivores can affect pollinator use of plants, pollinators, in turn, can affect the attack levels of seed and fruit feeders. Predispersal seed predators rely on successful fruit set to provision their developing larvae, and postdispersal seed predators rely on flowers to set fruit for adequate food resources. Thus, pollinator visitation to flowers may affect plant susceptibility to both predispersal and postdispersal seed predators. Leaving aside well-known instances of pollinators that also act as seed predators (i.e., yucca moths and fig wasps) (e.g., Aker & Udovic 1981, Pellmyr 1997), studies have found a positive link between pollination and predispersal seed predation (e.g., Cariveau et al. 2004, Herrera 2000), although this association is not universal (e.g., Ehrlén et al. 2002). The positive link between pollination and seed predation may be driven by two very different mechanisms. Seed predators may cue in on increased fruit and seed density associated with increased pollinator visitation, or pollinators and seed predators may use the same traits, such as flower number or

**TABLE 2** Multispecies effects on plant fitness or on selection on plant traits involving multiple herbivores and herbivores and pollinators

Interactors	Plant species (family)	Fitness component	Effects on fitness additive?	Nature of nonadditivity <sup>a</sup>	Plant trait(s) measured	Nonadditive effects on selection?	Reference
<b>Multiple herbivores</b>							
Above-ground and below-ground insect herbivores	<i>Lupinus arboreus</i> ( <i>Fabaceae</i> )	Growth and seed production	Yes		No trait examined		Maron 1998
Deer and mollusk herbivores	<i>Lupinus chamissonis</i> ( <i>Fabaceae</i> )	Survival and growth rate	Yes		No trait examined		Warner & Cushman 2002
Leaf miners and insect leaf herbivores	<i>Ipomoea purpurea</i> ( <i>Convolvulaceae</i> )	Seed production	Yes		Resistance to two herbivores, but never related traits to fitness		Hougen-Eitzman & Rausher 1994
Deer browsing, insect herbivore guild, fungal pathogen guild	<i>Ipomoea hederacea</i> ( <i>Convolvulaceae</i> )	Seed production	Not considered		Tolerance to herbivores, pathogens, deer	Yes	Stinchcombe & Rausher 2002
Simulated root and leaf herbivory	<i>Salix planifolia</i> spp. <i>planifolia</i> ( <i>Salicaceae</i> )	Biomass, leaf demography, and transpiration	Yes		No trait examined		Houle & Simard 1996
Eggplant flea beetle and horse nettle beetle herbivores	<i>Solanum carolinense</i> ( <i>Solanaceae</i> )	Fruits and seeds, fruit size, seed mass, germination, and root mass	Yes		No trait examined		Wise & Sacchi 1996 <sup>b</sup>
Above-ground and below-ground insect herbivores	<i>Tripleurospermum perforatum</i> ( <i>Asteraceae</i> )	Plant density and flower heads	Yes		No trait examined		Mueller-Schaefer & Brown 1995
Simulated deer browsing, seed flies, and caterpillars	<i>Ipomopsis aggregata</i> ( <i>Polemoniaceae</i> )	Seed, flower, fruit production	Yes = Browse/insect; No = Seed fly/caterpillar	Lesser	Flowering phenology	Yes (all three herbivores) No (just insects)	Juenger & Bergelson 1998
Spittlebug and leaf beetle herbivores	<i>Solidago altissima</i> ( <i>Asteraceae</i> )	Buds, leaves, roots, shoots and biomass	No	Greater (intensity of interaction depends on the response variable)	No trait examined		Hurbauer & Root 2002

Deer and leaf beetle herbivores and stem borers	<i>Rhus glabra</i> (Anacardiaceae)	Growth, seed production, and survivorship	No	Greater	No trait examined	Strauss 1991
Diamondback moth and flea beetle herbivores	<i>Brassica rapa</i> (Brassicaceae)	Seed production	No	Direction depends on densities of herbivores	Leaf area and resistance to the two herbivore species	Pilson 1996
Wire worm root herbivores and butterfly larval folivores	<i>Sinapis arvensis</i> (Brassicaceae)	Flowers, fruits, seeds and pollinator visitation	No	Lesser	No measured traits were related to fitness	Poveda et al. 2003
Spittlebugs and plume moth herbivores	<i>Erigeron glaucus</i> (Asteraceae)	Flower number	No	Lesser	No trait examined	Karban & Strauss 1993
Lodgepole pine cone borer moth, crossbills and squirrels	<i>Pinus contorta</i> var. <i>latifolia</i> (Pinaceae)	Seeds	Not addressed		Cone traits, resistance to predation	Selection on cone traits differed in habitats with differing seed predator communities, but nonadditivity could not be addressed Siepielski & Benkman 2004
<b>Herbivore-pollinator interactions</b>						
Insect florivores and supplemental hand-pollination <sup>c</sup>	<i>Castilleja indivisa</i> (Scrophulariaceae)	Seed number	Yes		No measured traits were related to fitness	Adler 2003
Floral herbivores and insect pollinators	<i>Helianthus foetidus</i> (Ranunculaceae)	Recruits in the next generation in the field	No	Detrimental effects of herbivores only in presence of pollinators; positive effects of pollinators only in the absence of herbivores	No trait examined	Herrera et al. 2002
Insect and ungulate fruit-feeders and insect pollinators	<i>Paeonia broteroi</i> (Paeoniaceae)	Seed set in the field	No	Detrimental effects of herbivores only in presence of pollinators; positive effects of pollinators only in the absence of herbivores	No trait examined	Herrera 2000

(Continued)

TABLE 2 (Continued)

Interactors	Plant species (family)	Fitness component	Effects on fitness additive?	Nature of nonadditivity <sup>a</sup>	Plant trait(s) measured	Nonadditive effects on selection?	Reference
Insect and ungulate fruit-feeders and insect pollinators	<i>Erysimum mediolispanicum</i> (Brassicaceae)	Seed set in the field	Not addressed		Plant height, floral shape, flower number	Selective effects of pollinators only present when browsers absent; selective effects of browsing reverse direction of selection on some traits; non-additivity not addressed	Gómez 2003
Simulated deer browsing and supplemental hand-pollination <sup>d</sup>	<i>Ipomopsis aggregata</i> (Polemoniaceae)	Seed set, flower and fruit production	No	Effects of herbivory on fitness mediated by pollination intensity	Flowering phenology, plant size, plant height		Juenger & Bergelson 1997
Simulated browsing and emasculation to prevent self-pollination <sup>d</sup>	<i>Ipomopsis aggregata</i> (Polemoniaceae)	Seed set, flower and fruit production	No	Benefits of emasculation only in the absence of damage	No traits examined		Juenger & Bergelson 2000
Simulated leaf herbivory and supplemental bee hive pollinator additions	<i>Cucurbita melo</i> (Cucurbitaceae)	Fruit number and mass	No	Effects of herbivory on fitness mediated by pollination intensity	No trait examined		Strauss & Murch 2004

<sup>a</sup>Expected based on additive effects of species. Lesser = impacts of interactors on plant fitness in combination less than would be predicted from pairwise interactions. Greater = impacts of interactors on plant fitness in combination greater than would be predicted from pairwise studies.

<sup>b</sup>In Wise & Sacchi (1996), for both root mass and seed germination, a marginal but not a statistically significant interaction occurred between the two herbivores.

<sup>c</sup>*Castilleja indivisa* is primarily bumblebee pollinated.

<sup>d</sup>*Ipomopsis aggregata* is primarily hummingbird pollinated.

flower size, to select plants (especially in cases where seed predators oviposit on flowers before or during the pollination stage) (e.g., Brody 1992). By experimentally manipulating pollination (either by excluding pollinators from flowers or by hand-pollinating flowers), one may possibly disentangle the two mechanisms.

In an experimental study with the perennial herb *Paeonia broteroi* (Paeoniaceae), Herrera (2000) found a significant interaction between pollinator and "herbivore" exclusion treatments for seed production. Mammalian fruit predators (referred to as "herbivores") fed exclusively on fruits from flowers that had been exposed to pollinators and ignored fruits produced from self-pollinated flowers. Similarly, in *Castilleja linariaefolia* (Scrophulariaceae), pollen supplementation to flowers, to mimic increased hummingbird-pollinator visitation, resulted in a marginal, although not statistically significant, increase in predispersal seed predation by plume moth larvae and fly larvae (Cariveau et al. 2004). In both of these studies, seed predators may have cued in on increased fruit and seed abundance associated with increased pollinator visitation or plant investment in fruit quality. Thus, when the effects of pollinators and seed predators are combined, seed predators may mask any plant-fitness benefits related to increased pollination (see also Gómez 2003).

In the case of granivory and frugivory, the link between increased pollination and increased seed predation has not been empirically measured, to our knowledge. Evidence suggests that seed-addition experiments increase seedling recruitment (Turnbull et al. 2000) and that granivores respond to increased seed abundance (Edwards & Crawley 1999) and strongly affect plant recruitment (Edwards & Crawley 1999, Maron & Simms 2001). Similarly, pollination also affects the quantity and quality of fleshy fruits (Gonzalez et al. 1998), and such variation can have sizable effects on the foraging behavior of frugivores (Moegenburg & Levey 2003). However, studies are rare that have manipulated pollination and measured subsequent fruit and seed risk to, or response of, granivores or frugivores.

**ENDOPHYTE-HERBIVORE INTERACTIONS** Defense mutualisms, such as those between plants and endophytes, can have a variety of effects on the host plant, which include increased resistance to herbivores and pathogens (Clay 1988). The endophytes of many cool-season agronomic grasses, such as *Festuca arundinacea* (Poaceae) and *Lolium perenne* (Poaceae), produce alkaloidal mycotoxins that increase plant resistance to invertebrate and mammalian herbivores in laboratory and field trials (Cheplick & Clay 1988, Clay 1988). Endophyte-mediated herbivore resistance is also found in other nongrass plant species (e.g., Raps & Vidal 1998, Saikkonen et al. 1996). For example, the cabbage plant *Brassica oleracea* var. *gemmifera* (Brassicaceae), when inoculated with an unspecialized endophyte (*Acremonium alternatum*), supported lower growth rates and survival of the diamondback moth larvae *Plutella xylostella*, potentially because of endophyte-mediated changes in plant phytosterol metabolism (Raps & Vidal 1998). However, endophyte-mediated resistance to herbivory is not universal (e.g., Faeth & Hammon 1997), and some studies have shown that plant-endophyte interactions

may even benefit herbivores (Gange 1996, Saikkonen et al. 1999). For example, the mean relative growth rate of grasshoppers was higher on the native grass *Festuca arizonica* (Poaceae) infected with *Neotyphodium* endophytes compared with uninfected *F. arizonica* (Saikkonen et al. 1999). Some of the ambiguity in endophyte effects on plant-herbivore interactions may be driven by the host plant (e.g., native versus agronomic versus exotic, grass versus tree), endophyte, and herbivore involved, as well as by environmental conditions and other species in the community (e.g., predators of herbivores) (Faeth 2002). Multiple types of fungal infections can also influence the effects of endophytes on herbivore and plant performance. For example, the beneficial effects of the foliar endophyte *Neotyphodium lolii* on perennial ryegrass (*Lolium perenne*) was reduced by mycorrhizal fungal infection (Vicari et al. 2002). Despite the contrasting results of these studies, the growing body of literature on endophytes suggests that these fungi provide an additional component of variation in the nature and strength of plant-herbivore interactions. To our knowledge, no study has examined the relationship between endophyte infection and impacts on pollination.

**HERBIVORE-MYCORRHIZAL INTERACTIONS** Mycorrhizae are fungi that have hyphal associations with the roots of many plant species. The fungi receive carbon from the plant and plants receive inorganic nutrients, especially phosphorus, from the fungi (or nitrogen if the fungi are ectomycorrhizal). In infertile soils, nutrients taken up by the mycorrhizal fungi can lead to improved plant growth and reproduction, and mycorrhizal-infected plants are often better able to tolerate environmental stresses and competition than are non-mycorrhizal-infected plants (for comprehensive information, see van der Heijden & Sanders 2002). However, the nature of mycorrhizal relationships with host plants ranges from mutualistic to parasitic, and the biotic and abiotic environment usually alter the plant/fungal relationship. The complexity of interactive effects is more extreme when the plant-fungal-herbivore relationship is considered (Gange et al. 2002). For example, in low-phosphorus environments, we expect mycorrhizal fungi to increase phosphorus uptake in the plant and to increase plant performance. Herbivore performance, in turn, may also increase with infection under these conditions (Gange et al. 1999). Thus, mycorrhizae may indirectly benefit herbivores by increasing the quality of the host plant. However, under stressful conditions, both herbivores and mycorrhizae may compete for plant resources (Gange et al. 2002, Gehring et al. 1997). Such conditionality may be one reason why mycorrhizal infection does not result in any predictable effects on herbivore performance (reviewed in Gehring & Whitham 2002). Interestingly, infection with arbuscular mycorrhizal (AM) fungi is much more likely to affect herbivore performance than ectomycorrhizal (EM) fungi, although, again, the directionality of this effect is inconsistent (Gehring & Whitham 2002).

Another reason for the inconsistency in herbivore response to mycorrhizal infection may lie in the fact that infection causes changes in both nutritive and defensive leaf chemistry (Gange & West 1994, Goverde et al. 2000). These changes, in turn, may differentially affect specialist and generalist herbivores. The performance of



generalist herbivores is often more sensitive to changes in defensive chemistry than is the performance of specialist herbivores, and, although sample sizes are small, Gehring & Whitham (2002) provide some evidence from a survey of studies that generalist insects may be more affected by fungal symbionts than are specialist insects. Responses of generalist and specialist herbivores to infected plants are complex, however—both the level of infection and the species composition of AM fungi influenced the performance of a specialist lepidopteran herbivore on *Lotus corniculatus* (Fabaceae) (Goverde et al. 2000). In summary, mycorrhizal infection can clearly alter the likelihood and intensity of plant interactions with herbivores, but the highly conditional nature of the plant-fungal interaction, coupled with the diverse responses of herbivores to changes in plant chemistry, mean that such effects may be idiosyncratic.

When herbivores, as opposed to fungi, are the first interactor with the plant, herbivory affects the likelihood and extent of subsequent mycorrhizal colonization of the shared host. Again, Gehring & Whitham (2002) reviewed the literature on herbivore-mycorrhizal interactions and found that in 28 of 42 cases, herbivores inhibited the colonization of mycorrhizae that shared the same host; in 11 cases, no effects occurred, and in 10 cases, herbivory facilitated the colonization of mycorrhizae. Herbivores may also affect the species composition of mycorrhizal communities (Eom et al. 2001, Gehring & Whitham 2002). To the best of our knowledge, no studies have examined the interactions between mycorrhizal fungi and pollinators. However, one could imagine that fungi could consume plant carbon that might otherwise sweeten nectar for pollinators. The converse might also hold: mycorrhizal-infected plants with greater nutrient uptake and greater growth rates might produce higher-quality nectar, larger flowers, or a larger floral display. Similar effects of mycorrhizal infection may influence fruit quality and the use of fruit by seed dispersers.

In summary, because plants are dynamic, living resources, interactions with other organisms elicit responses that influence simultaneously and subsequently interacting species of all types. Ample evidence suggests that the intensity or likelihood of interactions changes with the suite of interacting species. Plant responses to interactors may carry fitness costs (Koricheva 2002). Thus, for example, the benefits of deterrence of future herbivores may be offset by the costs of induced resistance. Only a few studies have examined the relative costs (energetic and ecological) and benefits (ecological) of induction simultaneously (Agrawal 2000, Baldwin 1998, Hare et al. 2003, Sagers & Coley 1995, Valverde et al. 2003). These costs and benefits ultimately are assessed with respect to the same bottom line: a change in plant fitness as a result of multispecies interactions.

### Criterion 3: Multiple Interactors Have Nonadditive Effects on Plant Fitness or on Selection

Despite the copious evidence that patterns of host-plant use are altered by other plant-animal (or animal-animal) interactions, we have much less evidence that

these altered interactions have effects on plant fitness. However, effects of multiple species on mean fitness alone in treatments cannot tell us anything about the nature of selection, because selection, by definition, is the relationship between a trait and fitness (for further discussion, see Juenger & Bergelson 1998, Stinchcombe & Rausher 2002, Strauss et al. 2004). The original wording of this criterion in Hougen-Eitzman & Rausher's (1994) seminal paper states that nonadditive effects of species on plant fitness provide evidence for diffuse selection. In this case, the authors measure two traits (resistances to two herbivores) but do not relate leaf area removed by each herbivore to plant fitness (selection on resistance); they analyze mean individual plant fitness in different communities. In a subsequent paper, Iwao & Rausher (1997) develop an extremely thorough theoretical and empirical treatment for analyzing selection gradients that relate fitness to resistance as a function of additive and nonadditive effects of community members. Thus, whereas the experimental and analytical approaches both test the effects of communities on selection and evolution, the verbal description of the criteria remained unchanged. In fact, to our knowledge, only six papers actually measure how selection changes in response to community composition: Pilon (1996), Iwao & Rausher (1997), Juenger & Bergelson (1998), Gómez (2003), Tiffin (2002), and Stinchcombe & Rausher (2002). Five of these papers document nonadditive effects of community members on selection on a focal trait or species. Because the initial criteria for evidence of diffuse evolution did not explicitly define the importance of linking traits to plant fitness, or of assessing the relative fitness of different genotypes in the different communities, many investigators have misunderstood the basic approach required to document diffuse selection or diffuse evolution (e.g., see several studies included in Table 2).

It is important to reiterate that nonadditive effects of community members on mean fitness in treatments may still have important implications for the ecological consequences of multispecies interactions through changes in population size and may affect community-level properties, such as trophic cascades (e.g., Peckarsky & McIntosh 1998) or biodiversity (Mueller-Schaerer & Brown 1995).

**MEASURING THE CONSEQUENCES OF MULTIPLE-SPECIES INTERACTIONS ON PLANT FITNESS** When plant fitness is to be measured in response to multispecies interactions, one question is essential: What is the most appropriate plant response variable to measure? In part, this decision depends on the aim of the study and whether the study includes both ecological and evolutionary perspectives.

Typically, studies have focused on measuring some correlate of plant fitness, such as plant growth, survival, flower production, pollen receipt, or seed production [hereafter referred to as fitness components (Campbell 1991)]. In many cases, however, plant-animal interactions directly and indirectly affect multiple, sequential fitness components (Adler et al. 2001), and total plant fitness may be differentially sensitive to particular fitness components (Ehrlén 2003). In addition, tradeoffs may occur between the components. For example, a large increase in seed

production by a perennial plant in one year may be countered by lower growth, survival, or reproduction in subsequent years (Ehrlén 2002, Primack & Hall 1990). In addition, male fitness components (seeds sired) and female fitness components (seeds produced) are not always affected similarly by the same interaction. For example, male reproductive success may be more strongly affected by herbivory (Strauss et al. 2001) or pollination (Stanton et al. 1991) than female reproductive success, although there are exceptions (e.g., Irwin & Brody 2000, Krupnick & Weis 1999).

Fitness components, such as seed production (a female component), may have ecological effects as long as a link exists between seed production and subsequent population size. In this case, multispecies interactions may drive plant population persistence, spread, and dynamics. In contrast, fitness measured through male function does not necessarily have effects on population size (a single male could sire all the seeds, but the numbers of seeds could remain constant if resource limitation, as opposed to pollination, sets bounds on seed numbers). Fitness through male function may have important evolutionary effects, however, because soft selection can occur in a population of constant size when allele frequencies within the population change. Thus, the choice of fitness components to be measured might be influenced by the motivation of the study, that is, whether the goal is to examine multispecies effects on plant population size or on selection on plant traits.

#### EXPERIMENTAL APPROACHES TO MEASURING THE COMBINED EFFECTS OF MULTIPLE INTERACTORS

**Fully-crossed factorial designs** An experimental approach is the most straightforward means of testing for nonadditive effects of multiple visitors on plant fitness or reproduction. To measure selection, trait measurements are also necessary. By experimentally manipulating each of the interacting players in a fully-crossed design, the individual and combined effects of visitors on plant fitness and on selection can be assessed. If one wants to explore selection by communities on a particular trait, one can regress values of the trait in question against the relative fitness of genotypes or plant families (or against fitness of individuals randomly assigned to treatments for phenotypic selection gradients). Such an approach allows exploration of selection gradients in treatments in which the presence or absence of interactors has been manipulated. Iwao & Rausher (1997) discuss in detail the theoretical considerations, experimental design, and statistical analyses to partition selection on a trait by a suite of interactors into diffuse versus pairwise components. These kinds of experiments give us insights into how evolution of traits may be influenced by a community context.

**The demographic responses to multispecies plant-animal interactions** Fully-crossed factorial designs such as those described above and below, and in which mean fitness of individuals in treatments is the sole response variable measured, in

some cases may tell us about the effects of communities on the population dynamics of component species. A handful of studies demonstrate that changes in fitness or reproduction as a result of multispecies interactions translate into changes in population size. For example, in an ambitious long-term study, Herrera et al. (2002) found nonadditive effects of pollinators and herbivores on plant fitness that translated into different numbers of seedling and adult recruits in populations of *Helleborus foetidus* (Ranunculaceae) that belonged to different experimental treatments. In addition, experimental flower removal and early-season defoliation negatively affected the population growth rate of *Primula veris* (Primulaceae) (García & Ehrlén 2002). Maron & Simms (2001) found that although exclusion of rodent granivores increased seedling emergence of *Lupinus arboreus* (Fabaceae), such effects were only marginally evident after three years (because of cutworm herbivory on seedlings). These studies suggest that multispecies plant-animal interactions can scale up to have population-level consequences in some (Ackerman et al. 1996, Louda & Potvin 1995), but not all, cases (Crawley & Nachapong 1985, Eriksson & Ehrlén 1992).

The above works are commendable in their long-term study of the effects of community composition on the populations of focal species across multiple generations. How single-year, short-term effects on seed production or growth influence population dynamics is difficult to determine because a correlation between increased seed production and future population size cannot be assumed. Several processes uncouple seed numbers from future plant population size; two processes are safe-site limitation (Crawley & Nachapong 1985, Eriksson & Ehrlén 1992, Maron et al. 2002) and self-thinning (e.g., Akifumi 1996). Thus, seed inputs do not always affect levels of adult plant recruitment (reviewed in Turnbull et al. 2000). These demographic links are only now beginning to be explored in detail (e.g., García & Ehrlén 2002, Louda & Potvin 1995, Maron & Gardner 2000, Turnbull et al. 2000), and this area of plant ecology is sorely lacking in empirical data (but see Maron et al. 2002, McEvoy et al. 1993, and references above).

Several caveats to the interpretation of demographic studies should be considered. Because rare long-distance dispersal events may be important to the founding of new populations and range expansions, and because these rare events are extremely difficult to assess in field studies, how levels of seed inputs affect them is difficult to determine. Even for wind-dispersed seeds, the vast majority of seeds are deposited very near the parent plant (Augsburger & Kitajima 1992). Local dynamics are what we can see and measure. Thus, we do not know the degree to which differences in seed production affect the incidence of important rare events, such as the establishment of new populations. Yet, these events clearly have large ecological impacts and fitness benefits when they occur. Similarly, we tend to measure seedling emergence but have a much weaker grasp on the meaning of seed inputs to seed-bank populations, which may also play important roles in population persistence (e.g., Kalisz & McPeck 1992). The effects of multispecies interactions on the population dynamics of plants and on plant-range limits and distributions need much more empirical attention.

**Additive versus nonadditive effects of multiple interactors on plants** Factorial experiments can tell us whether the effects of species together differ from those we would expect on the basis of their separate effects. As indicated by the studies summarized in Table 2, multispecies effects on plant fitness, growth, or reproduction often cannot be predicted from knowledge of the effects of each species in isolation. For example, *Trirhabda* beetles and *Philaenius* spittlebugs feeding together on the tall goldenrod *Solidago altissima* (Asteraceae) reduce the mass of the apical bud and the foliage more than would be expected from either insect feeding alone (Hufbauer & Root 2002). Similarly, Longland et al. (2001) show that the beneficial effects of larder hoarding by rodents on seed germination of Indian ricegrass are only evident in plots that also experience scatter hoarding by Merriam's kangaroo rats (*Dipodomys merriami*). When pollinators are limiting, effects of fruit-feeding herbivores are diminished (Herrera 2000, Herrera et al. 2002). The few studies that have addressed selection in response to community composition also show possible nonadditive, selective effects of community members. In *Ipomopsis aggregata*, a self-incompatible monocarp, browsing causes increased branching and flower production. However, pollinator limitation curtails fitness responses to damage from browsers in some years, and investigators found that selection on resistance to browsing may be diminished by pollinator responses (Juenger & Bergelson 1997). Alternatively, the relationships among plants and pollinators weaken when resource limitation overrides pollinator limitation in damaged plants (Juenger & Bergelson 1997). Browsers can also negate the selective effects of pollinators on plant height and corolla shape by removing flowers and fruits (Gómez 2003).

In summary, community composition significantly affects plant fitness, growth, or reproduction in the majority of experiments that have explored this question through the use factorial experimental designs (Table 2). The results from studies on the effects of multiple herbivores are mixed; about half show independent effects of herbivores on plant fitness (e.g., additive effects of herbivores on plant reproduction). Also, when nonadditive effects on plant fitness do occur, they are not consistent in direction. For example, in some cases, joint attack results in less fitness loss than would be predicted from the separate effects of each herbivore, whereas in other cases, the reverse is true. Although sample sizes are small, five of the six studies in Table 2 that have examined cumulative effects of herbivores and pollinators on plant fitness have found nonadditive effects.

We had a difficult time finding factorial experiments that examined the separate and combined effects of multiple-pollinator or multiple-seed-disperser species on plant fitness; this outcome likely reflects the difficulty of experimental manipulation in some of these systems (see below for other approaches).

**Alternative approaches to measuring multispecies effects on plants** Although experimental manipulations have the advantage of disentangling the individual and combined effects of multispecies interactions by application of standard experimental tools (i.e., factorial designs), this approach has limitations. Some interactions are very difficult to manipulate, most notably interactions among plants and

multiple species that have similar body size and activity patterns. For example, when pollinators have the same body size, phenology, and foraging behavior (i.e., comparing the individual versus combined effects of two bumblebee species), it is often difficult to exclude only one pollinator. In complex systems, so many species pairs may exist that fully-crossed factorial designs and replication of treatments would be logistically impossible. In such cases of intractability, there are other ways of attacking these problems.

Several approaches employed to examine interaction strengths of species in complex communities have been reviewed (Wootton 2002). Typically, the response variables for measuring interaction strengths are per capita growth rates or changes in population size. Some of these same techniques can be applied to evolutionary questions for which the response variable is the fitness of a focal species. Path analysis (reviewed in Shipley 2000) combined with structural-equation modeling (SEM, reviewed in Mitchell 1993) provides an additional approach for quantifying multispecies effects on plant fitness. Path analysis allows the dissection of complicated webs of direct and indirect effects among multiple interactors by use of a set of *a priori* hypotheses (Kingsolver & Schemske 1991, Mitchell 1993) and is particularly useful for generating hypotheses about the causal mechanisms of selection in systems where experimental manipulation is impractical (Grace & Pugsek 1998; but see Smith et al. 1997). Path analysis is a sequence of multiple regressions and correlations structured by *a priori* hypotheses regarding the causal relationships among variables (Mitchell 1993). The degree to which a path model provides an appropriate fit to the observed data can be tested by SEM. SEM tests the observed correlation structure in the data against the expected correlation structure in the path model through the use of a goodness of fit test (reviewed in Mitchell 1993).

Path analysis in combination with SEM can be used in a number of different ways in ecological and evolutionary studies. First, path analysis combined with SEM can be used to compare multiple, hypothesized causal structures in communities (Cariveau et al. 2004, Gómez & Zamora 2000). Second, given a particular causal structure, the relative strength of different direct and indirect effects of multiple agents can be separated and compared (Adler et al. 2001, Schemske & Horvitz 1988). Within the context of natural selection, path analysis combined with multiplicative fitness components are a powerful, multivariate approach by which to dissect and understand complex patterns of selection (Conner 1996), and path analytical techniques can help reduce environmental bias when estimating natural selection (reviewed in Stinchcombe et al. 2002) by including environmental "condition" variables in the path models (Scheiner et al. 2002). Alternatively, environmental bias can be reduced by estimating selection that uses genetic or family means from genetic replicates (e.g., Iwao & Rausher 1997).

Path analysis is increasingly used in studies of multispecies plant-animal interactions (e.g., Adler et al. 2001, Cariveau et al. 2004, Gómez & Zamora 2000, Juenger & Bergelson 1997, Mothershead & Marquis 2000, Schemske & Horvitz 1988) to evaluate the direct and indirect effects of multiple interactors on plant

fitness. Mothershead & Marquis (2000) used experimental manipulations combined with path analysis to compare the direct effects of leaf damage to *Oenothera macrocarpa* (Onagraceae) through decreased resource availability with the indirect effects of leaf damage through changes in floral characters and plant-pollinator interactions. In this system, the magnitude of the indirect effects of herbivory on changes in plant-pollinator interactions and plant fitness outweighed the direct consumptive effects of herbivory on plant fitness. Conversely, the direct effects of bud herbivory to *Castilleja indivisa* (Scrophulariaceae) on seed production outweighed the indirect effects of herbivory through changes in floral characters and plant-pollinator interactions (Adler et al. 2001). One common theme running through both studies, however, is that the direction or magnitude of effect of one interactor (i.e., pollinators) is dependent on the direction or magnitude of the other (i.e., herbivores). Studies in multispecies plant-animal interactions also include path analysis to estimate causal mechanisms of selection. In *Castilleja linariaefolia*, the strength of selection on calyx length, flower production, and plant height was greater for pathways through seed predation than for pathways through pollination because seed predators had strong negative effects on relative seed set compared with the weak benefits of pollinators (Cariveau et al. 2004). In southeastern Spain, *Hormathophylla spinosa* (Brassicaceae) experiences positive pollinator-mediated selection for flower number per plant and flower density in populations with low ungulate herbivory. However, in populations with high ungulate herbivory, the direct negative effects of herbivores on relative plant fitness masked any beneficial effects of flower number in attracting pollinators, and in one population with high herbivore pressure, plants experienced conflicting selection pressures between maximizing pollination and minimizing plant risk to herbivory (Gómez & Zamora 2000).

Despite their advantages, path analysis and SEM have limitations (for a more complete listing of limitations, see Mitchell 1993). First, path analysis should not be used to infer causation among variables (Mitchell 1993, Wootton 1994). Rather, path analysis identifies important correlations among variables and possible targets of selection that can be further tested experimentally (Kingsolver & Schemske 1991, Petraitis et al. 1996). Second, path analysis and the magnitude of path coefficients are strongly conditional upon which variables are included in the path model. Because the coefficient estimates from path analysis depend on the causal path structure, they do not produce selection gradients that can be used to predict evolutionary response to selection (Scheiner et al. 2000). Third, as it has been currently used, path analysis does not quantify nonadditivity of interactions on plant fitness. However, cross-product terms might possibly be incorporated into a path analysis to examine nonadditive effects of interactors on plant fitness. For example, one might include the cross-product term between honeybee visitation and butterfly visitation in a multiple regression that relates visitation rate to seed set. Similarly, nonlinear effects of interactors on plant fitness could be included by use of quadratic terms in the regressions. Approaches that integrate a variety of techniques, such as experimental tests of hypotheses developed from path analysis,

may provide the most promising avenues for understanding and predicting the selective effects of multispecies interactions in natural communities.

Along with path analysis, other approaches are also being explored. A recent paper has used optimality models to show that the degree to which a plant exhibits specialized traits for one interactor is bounded by the cost of this adaptation in its relationship with other interactors (Aigner 2001). Under this scenario, adaptations to uncommon or relatively ineffective interactors may occur as long as the cost is minimal. This approach speaks to the importance of experiments that elucidate costs of traits in the absence of species interactions, in addition to benefits in the presence of species interactions in factorial design. To examine evolution as a function of community membership in this context, manipulative experiments are required to exclude various species from focal plants. Fitness tradeoffs must be measured not only with respect to the mean plant phenotype but also across the whole range of phenotypic variation. The results of Aigner's (2001) model suggest that the criteria required for multiple species to affect trait evolution may be even broader than appreciated, although addressing these conditions experimentally will be at least as difficult as any of the previously discussed experimental approaches.

## FUTURE DIRECTIONS

Countless studies document the multifarious and diverse responses of community members to the actions of plant associates that precede them. These responses are typically mediated by plant reactions to the effects of previous interactors. Far fewer studies, however, document whether genetic correlations exist between traits important to interactions with multiple species, and even fewer studies hunt for genetic correlations between traits important in very diverse interactions (e.g., herbivore-pollinator, herbivore-competitor). We surmise that the latter is true because *a priori* mechanistic links between traits involved in diverse interactions are not always obvious. However, the presence of what we call "ecological pleiotropy," when the same trait influences very diverse interactions with multiple species, suggests that traits involved with diverse interactors may be more linked than we currently appreciate. As we understand more about the impacts of a trait on an interaction, its role in, or linkages to, other important agents of selection on the focal species may be worth exploring. Many traits that appear to be very important to plant fitness still exhibit heritable variation. We must, therefore, be open to considering links between these traits and the actions of diverse community members that may prevent fixation of favorable alleles specific to a single interaction (Rudgers 2004, Thompson 1994). Our review is unabashedly phytocentric. All the responses to selection have been measured in terms of the plant. For practical reasons, assessing plant fitness, and response to interactors, is much easier than assessing the fitness of plant associates, which may also be affected by the same multispecies interactions. For example, one could imagine that selection on the ability of an herbivore species (herbivore A) to detoxify plant chemical defenses may depend on the suite of herbivores that precede it in feeding on the host. In



some years or places, these predecessors may change and, by virtue of the different plant responses they elicit, they may either facilitate or impede the performance of herbivore A upon the plant. As far as we know, very little attention has been paid to the evolutionary responses of plant associates to the prior interactions a plant has had with other associates (but see Siepielski & Benkman 2004).

Another area that has received far less attention than it should is the effect of multiple interactors on selection on plant traits. Carrying interactions through to a thorough examination of fitness components requires time and energy (and is even more difficult for perennial plants that exhibit costs of reproduction in the following year). Moreover, these changes in fitness must also be related to consistent changes in trait values for us to compare selection in different community contexts. Studies that examine only fitness in response to multispecies interactions can inform us on the (potential) ecological effects of communities on population dynamics but not on differences in selection or evolution (for further discussion, see Strauss et al. 2004). Few studies have combined the measurement of traits with measures of plant fitness in this multispecies context (Table 2). Additional experimental approaches and analytical tools that will help us explore complex systems outside of factorial designs are likely to play a key role in the efforts to understand effects of communities on both ecological and evolutionary processes.

In summary, it is clear that ecological communities shape the traits of component species, not only through pairwise interactions between species but also through the joint actions of species that result in synergisms and alternate evolutionary trajectories. Multispecies effects may constrain the response of traits to selection and may be an important source of fluctuating selection that maintains genetic variation in ecologically important traits. In addition, multispecies interactions affect not only trait evolution but also, in the few studies that have examined it, the population dynamics of species within communities. We have a growing understanding that taking a community perspective will inform us of how multiple species together affect community structure and species diversity, as well as species evolution.

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