

Review

The evolutionary consequences of ecological interactions mediated through phenotypic plasticity

James A. Fordyce

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

e-mail: jfordyce@utk.edu

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Summary

Phenotypic plasticity describes the capacity of a genotype to exhibit a range of phenotypes in response to variation in the environment. Environmental variation encompasses both abiotic and biotic components of the environment, including interactions among organisms. The strength and outcome of many ecological interactions, ranging from antagonism to mutualism, are mediated through the phenotypically plastic responses of one or more players in the interaction. Herein, three broadly defined, non-mutually exclusive, evolutionary consequences of ecological interactions mediated through phenotypic plasticity are discussed. (1) The predictable plastic response of one partner can favor behaviors, physiological responses, and life history traits of an interacting partner that manipulate, circumvent, or ameliorate the response of that partner. (2) Phenotypic

plasticity can generate substantial spatial and temporal variation within and among populations. Such phenotypic variation can depend on the density and identity of interacting players in an ecological community, and can ultimately affect the evolutionary outcome of ecological interactions. (3) Phenotypic plasticity affects the strength and direction of natural selection. Ecological interactions mediated through phenotypic plasticity are ubiquitous in nature, and the potential evolutionary consequences of these interactions illustrate the complexity inherent in understanding evolution in a community context.

Key words: adaptation, coevolution, ecological interaction, herbivory, induced response, natural selection, phenotypic plasticity, predation, variation.

Introduction

Phenotypic plasticity refers to the ability of a genotype to exhibit alternative morphological, behavioral and physiological characteristics in response to environmental conditions (West-Eberhard, 1989; Garland, Jr and Kelly, 2006). The ability of an organism to respond to its surroundings can be critical for its success, especially in heterogeneous or novel environments, because it is a means for an organism to explore the adaptive landscape (Scheiner, 1993; Via et al., 1995; Price et al., 2003). Plasticity may also play an important role in evolution by governing or modifying developmental pathways (West-Eberhard, 2003). Thus, phenotypic plasticity plays a paramount role in generating the phenotypic diversity observed in nature.

Plasticity can affect both the mean and variance of a phenotype within a population (Fig. 1). A shift in the mean phenotype of a population can occur when all individuals in a population respond similarly to an environmental cue (Fig. 1A). The variance observed for a trait can similarly be reduced when a common response is observed among members of a population (Fig. 1B). Alternatively, the variance can increase if individual genotypes within a population respond differently to

the same cue (Fig. 1C). The influence of plasticity on the mean and variance of a population's phenotype will be influenced by the time scale over which plasticity is expressed, genetic variation for plasticity in the population, and heterogeneity of the environmental cues responsible for the plastic response.

The time scale over which a plastic response is expressed can be almost immediate, such as some physiological responses, behavioral responses of animals (West-Eberhard, 2003), and rapid movement of some plants (Forterre et al., 2005). Alternatively, plastic responses can be comparatively slow, such as morphological alterations exhibited by animals in response to diet (Wainwright et al., 1991; Price, 2006) or by plants in response to habitat (Ackerly et al., 2000). Plastic responses can also vary in their permanency. Some plastic responses, like behavior, are rapidly reversible, whereas other responses are developmentally fixed, such as the discrete mimetic morphs of *Nemoria arizonaria* (Geometridae) caterpillars (Greene, 1989). Many plastic responses fall between these two extremes and are at least partially reversible. The reversibility of a plastic response can be dependent on the ontogenetic stage when a response is induced. For example,

the reversibility of predator-induced morphologies exhibited by tadpoles decreases over development (Relyea, 2003). Induced phenotypes can be brief, or persist for years (Karban and Baldwin, 1997; Tollrian and Harvell, 1999), and may even persist across generations (Agrawal et al., 1999). The temporal dynamics of phenotypic plasticity can also present individual organisms with unique evolutionary challenges. For example, clouded sulphur butterfly larvae (*Colias philodice*) can feed on a range of legumes at early stages of development; however, they become obligate specialists on the plant species they consume during the penultimate instar (Karowe, 1989). Thus, over the course of their life, they experience the evolutionary and ecological trade-offs associated with a specialist and generalist diet (Futuyma and Moreno, 1988; Jaenike, 1990).

No organism is so insular that it does not have some interactions with other organisms, whether these interactions occur between members of the same or different species. The term 'interaction' describes how one organism affects another organism. The strength and direction of ecological interactions are ultimately determined by ecological conditions, including

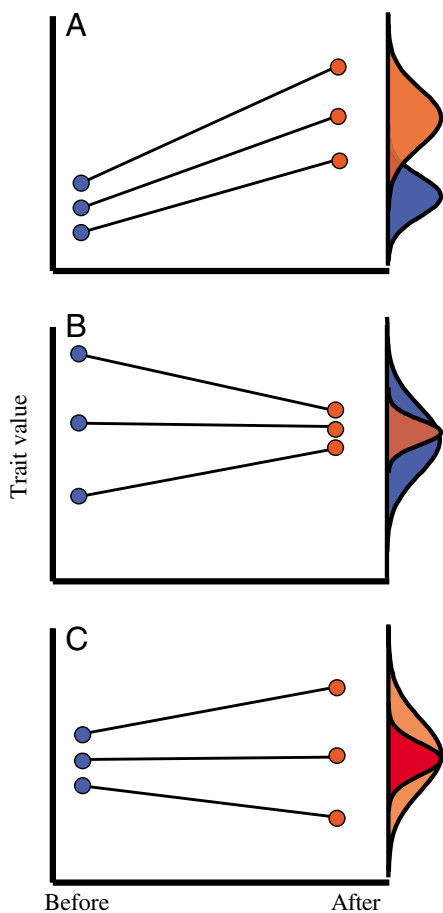


Fig. 1. Scenarios for change in mean and/or variance of a trait in a population between the constitutive phenotype expressed prior to an interaction (blue) and the induced phenotype following an interaction (red). (A) An increase in mean and variance of a trait. (B) Decrease in variance, mean unchanged. (C) Increase in variance, mean unchanged.

abiotic factors and the phenotypes of the participants. Interactions between organisms range from antagonism, such as those between predators and prey, to mutualism, such as those between plants and pollinators. The study of ecological interactions is challenging because the effect of the interaction on any given participant, whether it be positive, negative or neutral, often depends on the current ecological conditions (Thompson, 2005). The direction of an interaction may be antagonistic under one set of ecological conditions, yet neutral or beneficial under alternative conditions (e.g. Masters and Brown, 1992; Thompson, 1988; Nykänen and Koricheva, 2004). For example, the presence of ant-tended herbivores can actually be beneficial to a plant when the tending ants also defend the plant against other herbivores (Messina, 1981). From the perspective of the plant, the direction of the interaction depends on the presence or absence of other herbivore species that can cause severe damage. This rule of conditionality extends to interactions that are affected by phenotypic plasticity of one or more players in an interaction.

The role of environmental conditions affecting phenotypic variation in a population has long been recognized in basic additive genetic models, where phenotypic variation is partitioned between genetic effects and environmental effects. The contribution of environmental effects to phenotypic variation represents overall plasticity. The interaction between genotype and environment represents genetic variation for phenotypic plasticity. Although phenotypic responses to the environment may not increase reproductive success (i.e. fitness) and are often referred to as environmental noise, they still can be considered plasticity because alternate phenotypes are produced by the same genotype (Connor and Hartl, 2004; Garland, Jr and Kelly, 2006). Such non-adaptive, at times maladaptive, phenotypic responses can influence the strength and direction of ecological interactions and, therefore, can affect the fitness of one or more interacting partners. Adaptive plasticity describes phenotypic responses to the environment that results in increased fitness for an organism, such as inducible defenses of plants in response to herbivore attack (Karban and Agrawal, 2002).

Environmentally influenced phenotypic variation can be further partitioned between abiotic and biotic components of the environment. Here, the interaction term between abiotic and biotic environmental factors describes how plastic responses to an interaction can vary over different conditions. For example, the capacity of plants to respond to herbivore attack can be affected by nutrient availability (Lou and Baldwin, 2004). Biotic components of the environment include interactions with other organisms and will largely be the focus of the current discussion.

Many ecological interactions are mediated through the phenotypic plasticity of participants in response to other participants (Karban and Baldwin, 1997; Tollrian and Harvell, 1999; Agrawal, 2001; Werner and Peacor, 2003; Callaway et al., 2003; Miner et al., 2005). The strength and direction, and ultimately the outcome, of these interactions will be influenced by ecological conditions, including the genotypes involved in an interaction and the capacity for reciprocal phenotypic responses

among the participants (Agrawal, 2001). Many research programs have been dedicated to understanding plastic responses and ecological interactions, often in the context of induced resistance or defense observed in antagonistic interactions, such as immune responses to pathogens (Dangl and Jones, 2001), predator-induced morphology and behavior (Tollrian and Harvell, 1997; Preisser et al., 2005), and herbivore-induced plant responses (Karban and Baldwin, 1997). Mutualistic interactions can also be mediated through plasticity, for example by modifying the quantity or quality of rewards provided by one partner in the interaction (Leimar and Axen, 1993).

Plasticity can also be an important agent for indirect interactions among members in an ecological community. For example, damage caused by an herbivore can induce a plant phenotype that affects the performance of other herbivores (Masters and Brown, 1992; Denno et al., 1995; Viswanathan et al., 2005; Fordyce, 2006). Although many examples of phenotypic plasticity exhibited in response to ecological interactions have been shown to be beneficial, such as induced resistance or defense, this is not always the case. For example, some herbivore-induced plant responses can increase a plant's susceptibility to further attack (Underwood, 1998). Thus, spatially and temporally separated herbivores can have indirect interactions with each other mediated through the phenotypically plastic responses of the plant.

Phenotypic plasticity plays a substantial role in generating variation in the strength and direction of ecological interactions. In this review, I focus on the evolutionary consequences of interactions among species that are mediated through phenotypic plasticity. These consequences are separated into three, non-mutually exclusive, facets of interactions mediated by plasticity: (1) predictability of plastic responses, (2) spatial and temporal variation caused by plasticity, and (3) plasticity's effect on the fitness landscape and natural selection.

Predictability

Predictable plastic responses are those that are reliably expressed across environments following an interaction. Predictable plastic responses provide the opportunity for the evolution of strategies that ameliorate, avoid or manipulate the anticipated phenotypic response of an interacting partner. These strategies include behaviors, physiological responses and life-history evolution.

Many herbivores that feed on plants possessing laticifer systems disrupt latex flow prior to feeding by severing the latex bearing canals (Dussourd, 1993; McCloud et al., 1995). The ability of herbivores to anticipate latex exudation and manipulate the effectiveness of this plant response to damage can substantially influence herbivore diet breadth (Dussourd and Denno, 1994). Recently, it was shown that larvae of the corn earworm (*Helicoverpa zea*) adjust their physiology in anticipation of induced plant responses by 'eavesdropping' on the plant's physiology (Li et al., 2002). The larvae altered the quantity and quality of gut P-450 enzymes in response to plant salicylates and jasmonates, signaling compounds in plants

associated with the induction of defensive compounds. As a consequence, the larval gut was prepared prior to the induction of plant defensive compounds, thereby reducing the efficacy of the induced plant response.

The phenotypically plastic responses of a participant in an interaction can also be manipulated through life history traits. For example, large clutch size and aggregative feeding of larvae of the pipevine swallowtail butterfly (*Battus philenor*) can be an effective strategy for increasing host plant suitability, thereby accelerating larval developmental rate (Fordyce, 2003). The effectiveness of group feeding as a manipulative strategy varies among potential host plant species. Populations using host plants that cannot be manipulated through aggregative feeding usually lay substantially smaller clutches and larvae do not feed in dense aggregations (Fordyce and Nice, 2004). The ability of larvae to manipulate host plant quality through aggregative feeding might explain geographic variation in clutch size.

Many parasites manipulate the behavior of their hosts in ways that enhance parasite transmission and survival (e.g. Moore, 1984; Stamp, 1981; Lafferty, 1999), and for some parasites such behavioral manipulation is necessary to complete their life cycle. For example, Thomas et al. showed that a parasitic nematomorph induced a behavior in their insect host that caused them to enter the aquatic habitats required for the parasite's life cycle, even though the behavior is lethal for their host (Thomas et al., 2002). Various species of rust fungi manipulate the phenotype of their host plant, inducing the formation of structures called pseudoflowers that mimic the appearance of flowers. These floral mimics are visited by pollinators, which disperse fungal spores and facilitate cross-fertilization of mating types (Roy, 1993; Pfunder and Roy, 2000). Such strategies demonstrate that manipulation of plastic responses can affect both direct interactions between participants and indirect interactions among community members.

The ability to manipulate the phenotype of an interacting partner can provide an opportunity for entry into a novel adaptive zone, facilitating diversification of a lineage (i.e. 'key innovation') (Simpson, 1953). For example, the ability to form plant galls, structures formed by abnormal growth of plant tissues, has arisen in at least seven orders of insects and has led to an extraordinary adaptive radiation of some groups, such as gall wasps (Cynipidae) and gall midges (Cecidomyiidae) (Weis et al., 1988; Inbar et al., 2004). Gall formation is such an intrinsic quality of some insect life histories that the gall itself, an expression of the plant's genotype, can be regarded as the extended phenotype of the gall former (Dawkins, 1982). The ability to effectively manipulate the host phenotype, usually in very specific ways, restricts the host plant breadth of gall formers. As a consequence of this intimate association, nearly all gall-forming insects are extremely specialized for particular host plant species.

Spatial and temporal variation

The strength and direction of ecological interactions vary

in time and space. Genetic variation within and among populations can be an important determinant of phenotypic variation, which in turn can affect ecosystem processes (Madrictch and Hunter, 2002; Schweitzer et al., 2004) and play an important role in determining the composition and organization of ecological communities (Antonovics, 1992). For example, increased genetic variation in plant communities can lead to increased richness of arthropod communities (Wimp et al., 2004; Johnson et al., 2006). A key component of community genetics is the emphasis on the role of genetic variation affecting phenotypic variation within a community (Whitham, 2003). Phenotypic plasticity in response to ecological interactions can similarly play an important role in generating phenotypic variation within and among populations (Karban and Baldwin, 1997; Tollrian and Harvell, 1999; Roff, 1992; Agrawal, 2005).

Plasticity in response to ecological interactions can affect the mean of a population phenotype (Fig. 1). Predator threat can induce population-wide behavioral and morphological responses of their prey. For example, many amphibians and aquatic insect larvae adjust their behavior and morphology in response to predator threat (Benard, 2004). Predator-induced responses can persist in populations and extend beyond the community where they were induced. Wood frog tadpoles (*Rana sylvatica*) not only change morphology in the presence of predators in their aquatic environment, but emerging metamorphs have relatively long fore- and hindlimbs (Relyea, 2001). The chemical defenses of the western toad (*Bufo boreas*) metamorphs were higher when tadpoles were reared in the presence of predator cues (Benard and Fordyce, 2003). As a consequence of phenotypic plasticity, the mean phenotype of populations occurring in high predator environments might differ substantially from populations where predators are absent (Abrams, 1984; Tollrian and Harvell, 1999; Werner and Peacor, 2003; Preisser et al., 2005). For example, predator cues increased the level of tadpole aggregation and led to more synchronous metamorphosis of the American toad (*B. americanus*) (DeVito, 2003). Similarly, herbivore-induced responses can change the mean phenotype of a plant population, such as changes in nutritional quality, chemical defenses and structural defenses (Karban and Baldwin, 1997).

The variance of a trait can be reduced in a population in response to biotic interactions. Behavioral plasticity in response to predator threat can markedly reduce the size of a prey population's realized niche, reducing the range of occupied habitats and possibly the amount of available resources (Preisser et al., 2005). Other population responses to biotic interactions, such as premature leaf abscission of plants in response to herbivory (Simberloff and Stiling, 1987) and accelerated maturation or dormancy in response to predators (Lass and Spaak, 2003), also have the potential to greatly affect the variance of traits relevant to an interaction. An increase in phenotypic variance due to plasticity can result if individuals within a population respond idiosyncratically to an interaction or if genetically based variation in plasticity is present in the population. Idiosyncratic responses to an interaction, by definition, are not predictable. Thus, interacting partners must

be able to cope with a wide range of phenotypes and the evolution of manipulative strategies will be less likely, unless these strategies circumvent or prevent an induced response.

The mean and variance of phenotypic traits relevant to interactions can also be affected by the diversity of participants in the interactions. For example, prey may respond to predator threat by inducing behaviors or morphologies specific to a particular predator (Sih et al., 1998; Kishida and Nishimura, 2005). Similarly, the herbivore-induced phenotypes of plants can vary according to the identity of the herbivore. Herbivore-induced responses can range from increased resistance against further herbivory to increased vulnerability to subsequent attack, and can be specific to particular herbivore species. The identity of herbivores inflicting damage on the common milkweed (*Asclepias syriaca*) early in the season influenced which species of herbivores colonized the host plant later in the season (Van Zandt and Agrawal, 2004). Thus, plasticity can generate an important feedback between induced phenotypes and community composition. The assembly of an herbivore community on a plant can depend on the identity or density of particular community members that affect plant phenotype. Such community architects have been termed 'keystone herbivores' (Hunter, 1992; González-Megías and Gómez, 2003); analogous to Paine's 'keystone predator' concept (Paine, 1966). Removing a keystone herbivore results in an alternate plant phenotype, affecting the distribution and abundance of other community members, including herbivores and herbivore natural enemies.

Community composition, and thus phenotypic variation caused by plastic responses to interactions, varies in space. Within-population variation can be altered if there are multiple players involved in an interaction. Among-community geographical variation in the presence of important participants in an interaction, such as keystone herbivores, can increase among-population differences. Thus, plasticity in response to ecological interactions can generate patterns of phenotypic variation similar to that caused by genetic variation. Among-community variation in the strength and direction of interactions can profoundly influence geographic variation in evolutionary trajectories (Thompson, 1999; Thompson, 2005; Ridenhour, 2005).

The regularity with which particular ecological interactions occur varies among communities. Thus, some populations might consistently be involved in a particular interaction, such as competitive interactions between plant populations in the presence of a keystone herbivore, whereas other populations may not. Among-population phenotypic variation can be a consequence of the plastic responses unique to local conditions; however, these differences can eventually lead to genetically based differences (Pigliucci and Murren, 2003). For example, among-population variation was found in the propensity of spadefoot toad tadpoles (*Spea multiplicata*) to exhibit a carnivorous phenotype, a plastic response to the presence of particular prey items (Pfennig and Murphy, 2002). The carnivorous phenotype was more commonly expressed in populations that were not sympatric with the superior competitor, *S. bombifrons*.

The evolutionary outcome of biotic interactions, whether it

is the response of one participant in an interaction or coevolution, will be influenced by the phenotypic variation present for traits relevant to the interaction. If the population of one participant involved in an interaction has little phenotypic variation, all individuals of the interacting partner will be under similar selection pressure, facilitating adaptive evolution in the population. However, adaptive evolution in response to an interacting partner is more difficult when individuals within a population interact with different phenotypes. Phenotypic plasticity can play an important role in slowing the adaptive response of an interacting partner by providing a 'moving target' for natural selection (Adler and Karban, 1994). This basic principle has been used to retard the evolutionary response of insect pests and pathogens to genetically modified crops or pesticides (Rausher, 2001).

Natural selection, phenotypic plasticity and ecological interactions

Plasticity can affect the strength and direction of natural selection that occurs between interacting species. Natural selection affects the frequency distribution of phenotypes in a population. How a population will respond to selection can be graphically illustrated by plotting the phenotypic distribution of a trait against mean fitness (assuming no frequency dependence) (Lande, 1979; Lande and Arnold, 1983; Brodie et al., 1995; Price, 2006). If the adaptive surface remains unchanged, populations will evolve a mean phenotype that maximizes mean fitness. However, phenotypic plasticity of an interacting partner can result in dynamic adaptive surfaces that change over time in response to interactions (Fig. 2). In short, the fitness surface of one participant in an interaction can be determined by the plastic response of its partner.

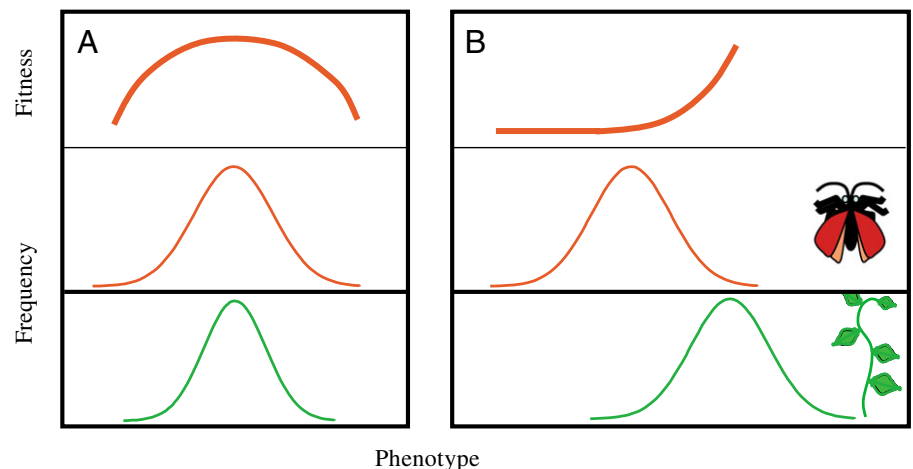
Plastic responses of one participant might favor a wider range of tolerance for that trait in its interacting partner. For example, herbivore-induced changes in plant chemistry might favor herbivore phenotypes that have tolerance or the ability

to cope with a broad spectrum of host plant chemistry (Fordyce, 2001). Similarly, plasticity of one partner might select for the capacity of the other partner to express counter plastic responses (Broadway, 1996; Agrawal, 2001; Kopp and Tollrian, 2003). The ability for reciprocal phenotypic plasticity will be important if the fitness of the constitutive phenotype is greatly reduced as consequence of plasticity in the interacting partner. Thus, plasticity expressed by one community member creates a variable biotic environment that might favor the evolution of plasticity in other community members.

The time scale over which plastic phenotypes are expressed will undoubtedly influence the evolutionary response of the interacting population. Whereas plasticity that plays an important role within a generation might favor broader tolerance or reciprocal plasticity, plastic responses in one species that extends over multiple generations of the other might lead to shifting selective pressures across generations. For example, changes in foliar chemistry of trees following herbivore outbreaks can persist for years, potentially spanning several insect generations (Haukioja, 1990; Karban and Baldwin, 1997). Thus, many insect herbivores experience periods of selection imposed by increased defensive chemistry, followed by a period of relaxed selection. Such temporal, across-generation, variation in the strength and direction of selection might be important for maintaining genetic variation in populations.

Plasticity in response to interactions can alter the relative contribution of genetic variation to phenotypic variation, and ultimately the strength and direction of selection. From an evolutionary perspective, this reduces the likelihood of strict, trait-for-trait pairwise coevolution between interacting partners, illustrating why diffuse coevolution is assumed to occur commonly in antagonistic interactions, such as those between plants and natural enemies (Rausher, 1996; Thompson, 1999; Inouye and Stinchcombe, 2001; Strauss and Irwin, 2004). Plasticity can affect a population's ability to respond to selection imposed by particular community members because the phenotypes expressed are conditional on prior interactions.

Fig. 2. A scenario where the plastic response of one partner affects the fitness surface of an interacting partner; here an example between an insect herbivore population and its host plant. The red curves indicate the phenotypic distribution (middle) and fitness surface (top) of the insect herbivore. The green curve indicates the distribution (bottom) of host plant traits relevant to the interaction. (A) Prior to the plastic response of the plant, the traits of the herbivore mirror those of the plant. If the phenotypic distributions remain constant, stabilizing selection will occur, selecting against extreme phenotypes with lower relative fitness. (B) A plastic response of the plants shifts the distribution of phenotypes in the population. As a consequence, the fitness surface of the herbivore changes and directional selection occurs. Note that it is possible for the herbivore to have a complementary plastic response, which will change its phenotypic distribution and the shape of the fitness surface.



Take a hypothetical example where early in a season the variation observed in a population for a trait relevant to an interaction is largely explained by genetic variation. The proportion of phenotypic variation that is explained by genetic variation describes the heritability of the trait, or the ability of the trait to respond to selection. Over the course of the season, the phenotypic variation present in the population is increasingly conditional on interactions with other community members accumulated over time. Thus, a consequence of plasticity can be temporal variation in the heritability of traits relevant to an interaction. Pilson observed genetic variation in goldenrod (*Solidago altissima*) for resistance to various herbivores that damage the apical meristem causing the plant to branch (Pilson, 1992). When branch-causing herbivores were present, the plant genotype predicted the distribution of aphids because aphids were more likely to be found on plants with multiple branches. However, when branch-causing herbivores were absent, aphids were randomly distributed among genotypes. Thus, the appearance of genetic variation for resistance to aphids was contingent on previous interactions with branch-causing herbivores.

Conclusions

The diverse interactions occurring in communities coupled with the conditional phenotypic responses of participants show that phenotypic plasticity can have profound evolutionary consequences, both within and among populations. When a plastic response of one interacting partner is dependably expressed, life history and behavioral strategies can evolve in anticipation of these predictable responses. The prevalence of such anticipatory strategies, including those that manipulate the phenotype of an interacting partner, remains to be seen. Phenotypic plasticity can generate patterns of variation similar to those resulting from genetic variation. What is unknown, however, is the relative importance of genetic diversity *versus* phenotypic plasticity in generating variation that influences the composition of ecological communities. Understanding the adaptive evolutionary responses of interacting partners requires an appreciation that plasticity determines the interacting phenotypes, and ultimately can mediate shifting selective pressures.

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