Evolution in a Community Context: Trait Responses to Multiple Species Interactions*

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ABSTRACT: Species that coexist in diverse natural communities interact in complex ways that alter each other's abundances and affect selection on each other's traits. Consequently, predicting trait evolution in natural communities may require understanding ecological and evolutionary dynamics involving a number of species. In August 2016, the American Society of Naturalists sponsored a symposium to explore evolution in a community context, focusing on microevolutionary processes. Here we provide an introduction to our perspectives on this topic by defining the context and describing some examples of when and how microevolutionary responses to multiple species may differ from evolution in isolation or in two-species communities. We find that indirect ecological and evolutionary effects can result in nonadditive selection and evolution that cannot be predicted from pairwise interactions. Genetic correlations of ecological traits in one species can alter trait evolution and adaptation as well as the abundances of other species. In general, evolution in multispecies communities can change ecological interactions, which then feed back to future evolutionary changes in ways that depend on these indirect effects. We suggest avenues for future research in this field, including determining the circumstances under which pairwise evolution does not adequately describe evolutionary trajectories.

Keywords: coevolution, diffuse selection, indirect effects, natural selection, species interactions.

Introduction

It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us. (Darwin 1859, p. 489)

Since Darwin's description of the tangled bank, biologists have described and studied the complexity of species interactions in natural communities. Early influential work, such as Levins's *Evolution in Changing Environments* (Levins 1968) and Endler's *Natural Selection in the Wild* (Endler 1986), have considered the forces that shape natural selection and evolution in complex natural environments. Over the course of a lifetime, individuals of any species are likely to interact with multiple resources, competitors, predators, parasites, and mutualists. These species interactions are a common currency between studies of ecology and evolutionary biology. Community ecologists concerned with the factors that determine the abundance, diversity, and distribution of species have been the primary explorers of the effects of multiple species interactions but have been less concerned with evolutionary changes in traits. By contrast, evolutionary biologists examining the causes of natural selection have traditionally focused on single species or pairwise interactions as agents of selection. How complex species interactions involving multiple direct and indirect effects influence natural selection and evolution has received less attention. These complex species interactions, however, are key to connecting the mechanistic processes that drive natural selection with an ecologically realistic synthesis of evolution in natural communities.

We refer to evolution that occurs in response to more than one species as evolution in a community context (terHorst et al. 2015; Weber et al. 2017). Although a community technically need be composed of only two species,

we refer to such two species communities as pairwise scenarios to distinguish them from the more complex features that arise in more species-rich communities. Whether evolution in a community context is worth studying depends on how important multispecies interactions (such as indirect effects) are for predicting evolutionary trajectories in natural communities. Even when intraspecific or pairwise interactions are the dominant selective agents in a community, indirect effects may cause those interactions to change when other species are present. Although cases where intraspecific or pairwise interactions explain the majority of the selection pressure on a focal trait likely occur in some scenarios, here we explain why incorporating interactions with more than one species can substantially alter our understanding of evolution in diverse communities. Such research is also critical for community ecologists because, in many cases, evolution on ecological timescales can feed back to affect species interactions that determine diversity, abundance, and distribution of organisms (Post and Palkovacs 2009; Schoener 2011; Reznick 2013).

At a recent meeting of the Ecological Society of America in Fort Lauderdale, Florida, the American Society of Naturalists sponsored a symposium titled "Evolution in a Community Context." In this symposium, we discussed the effects of multiple species interactions on microevolutionary processes. A recent review also highlights the effects of multiple species interactions on macroevolutionary processes (Weber et al. 2017). Here we provide a summary of the topics discussed in the symposium, placed in the context of the current research in this field. Other papers in this issue focus on each of these topics in greater depth. We also highlight possible avenues of future research for both ecologists and evolutionary biologists.

Our goal is to highlight some key aspects of evolution in a community context at the cost of not covering other important topics. We first describe how multiple direct interactions with more than one species affect adaptation to the whole community compared with pairwise scenarios. Second, we discuss how ecological indirect effects among species can result in evolution that cannot be predicted from direct interactions. Third, we consider how genetic correlations among traits that mediate an organism's response to the community can alter trait evolution and adaptation. Fourth, because evolution of multiple species in response to one another can alter ecological interactions between species, we describe how this feedback may alter predictions about both ecological and evolutionary processes. Finally, we provide avenues for future research in this field. Unfortunately, a thorough review of all topics related to multiple species interactions and evolution would not fit in the pages of this journal. Instead, we highlight the issues most relevant to other papers in this issue, although we acknowledge the importance of many other eco-evolutionary topics not discussed here.

Evolution in Response to Direct Interactions with Multiple Species

Much of the work to date on understanding species responses to natural selection has focused on a single species responding to an all-encompassing environment or to a pairwise interaction with one other species. This approach is a natural first step to understanding species evolution in more complex environments or when direct interactions between two species are much more important than interactions with other species. However, in scenarios in which a focal species is responding to selection pressure from multiple species, it is critical to understand the sum of these interactions in order to understand the evolutionary trajectory of the focal species.

Evolution of Multiple Competitors

Classic theory suggests that competing species will evolve to differentiate in their niches in order to coexist (Brown and Wilson 1956; Abrams 1986; Taper and Case 1992). Alternatively, differences in per capita rate of increase (r), tolerance of competition, or resource use efficiency (K) may also drive fitness differences among species that decrease coexistence (Chesson 2000). Evolutionary divergence in niche use may act as a stabilizing mechanism to facilitate coexistence, while more equal fitness can lead to niche convergence among species and facilitate coexistence or persistence (Chesson 2000; Levine and HilleRisLambers 2009; Lankau 2011). Most work on the evolution of competitors focuses on two competing species, but we can use this framework to make predictions for evolution in a multispecies context. Species in pairwise scenarios may diverge in their niche use, but this depends on niche use by other species (terHorst et al. 2010*b*). Evolution of multiple competitors can lead to optimal niche packing along a resource axis (MacArthur and Levins 1967; Case 1981), but the extent to which this occurs depends on environmental conditions and the number of species in the community (Scheffer and van Nes 2006; Fort et al. 2009). Species may clump together in niches, resulting in patterns of both niche divergence and convergence in a multispecies community context (Hubbell 2005, 2006; Scheffer and van Nes 2006; Fox and Vasseur 2008; terHorst et al. 2010*b*). In this issue, Schreiber et al. (2018) demonstrate that evolution can act as both an equalizing (minimizing fitness differences) and a stabilizing (minimizing niche overlap) mechanism that allows for coexistence among species.

In situations where all niches are filled, species must evolve to share resources in order to coexist. When niche divergence is not possible, the only viable evolutionary strategy is to reduce fitness differences with other species (Abrams 1986; Hubbell 2005, 2006). The likelihood of trait convergence may increase with the number of competing species

and be a viable alternative to extinction in multispecies scenarios. For example, if the breadth of resources available to all species in the environment is very narrow, the selective pressure to converge imposed by the environment can be greater than the selective pressures for niche divergence due to competition, thus causing species to converge in resource use (e.g., Kopp and Gavrilets 2006). In other words, convergence may be the lesser of two evils, evolutionary speaking; species may converge in their niche use because divergence would have led to greater niche overlap with another species that is a stronger competitor. These results can be realized only when considering indirect effects among multiple species evolving in response to one another (terHorst et al. 2010*b*).

Empirical tests of multiple competitors evolving in response to one another in natural communities reveal that the predictions above are likely too simplistic. Using a community of competing protozoa that live inside carnivorous pitcher plants, Miller et al. (2014) found that competitive interactions among some species increase over time, suggesting evolutionary convergence in niche use, while competitive interactions among other species decrease, suggesting evolutionary divergence in niche use. Interestingly, the initially competitive species evolved to be weaker competitors, while the initially poor competitors evolved to have stronger competitive effects (Miller et al. 2014). This result may be the outcome of frequency-dependent selection because of a trade-off between intra- and interspecific competition (Aarssen 1983; Travis et al. 2013). Competitively dominant species displace other species and tend to interact with more conspecifics and thus respond to intraspecific competition, while subordinate species experience more selection pressure from heterospecifics. In that sense, evolution in response to both inter- and intraspecific competition could result in coexistence among species (Lankau and Strauss 2007; Vasseur et al. 2011). Even in cases where intraspecific competition imposes strong selection pressure, multispecies interactions may alter the relative importance of intra- and interspecific competition in driving selection.

Diffuse Evolution in Response to Other Species

Species interactions are obviously not limited to competition but could involve a variety of positive and negative interactions with many different species. In pairwise interactions (e.g., predators, competitors, mutualists), one species often imposes selection on traits in another species that are directly related to that interaction (e.g., antipredator defenses, resource use, or attractiveness to mutualists; fig. 1). Janzen (1980) coined the term "diffuse coevolution" to describe the situation in which traits evolve in response to multiple species. When additional species are present in the community, the additional species may or may not alter the trait evolu-
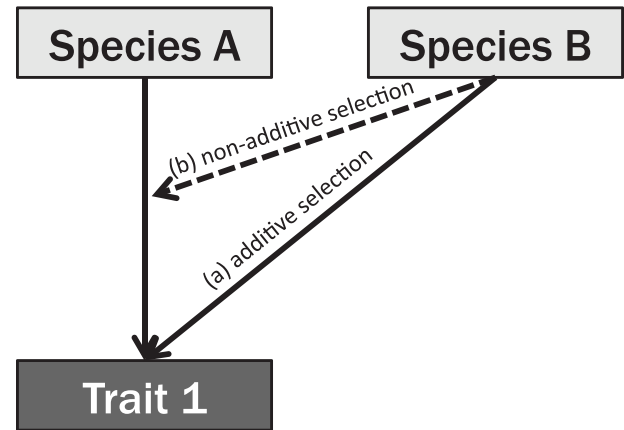

Figure 1: Evolution of a trait in a focal species in response to species A may be affected in various ways by the presence of species B: B imposes additional selection on trait 1 (*a*) or B alters the selection imposed by species A (*b*). A color version of this figure is available online.

tion observed in the pairwise scenario (fig. 1). There is now a body of theoretical and empirical work that quantifies trait evolution in response to more than one species, although the relative importance of pairwise evolution or evolution in a community context varies (reviewed in Rausher 1996; Strauss and Irwin 2004). For example, Tiffin (2002) quantified selection on antiherbivore defenses in morning glories and found that selection in response to herbivores was similar regardless of whether a crabgrass competitor was present. In contrast, Gómez (2003) found that pollinators imposed selection on flower number in *Erysimum mediohispanicum*, but that such selection could not be detected when ungulate herbivores were also present.

Deviations from pairwise evolution (i.e., diffuse evolution) result when evolution in the presence of one species is altered by the presence of a second species (Hougen-Eitzman and Rausher 1994; Iwao and Rausher 1997; Strauss et al. 2005). This can occur additively when the second species imposes selection independently of the first and neither species alters selection imposed by the other (terHorst et al. 2015; fig. 1). However, if the second species imposes indirect ecological effects, in which it alters the nature of the effect of the first species, nonadditive selection can result (Inouye and Stinchcombe 2001; terHorst et al. 2015, 2017; fig. 1). In the case of either diffuse or nonadditive selection, trait evolution will be adaptive with respect to the entire community context, but traits may not be adaptive with respect to any single interacting species. For example, production of a costly antipredator defense may limit the competitive ability of an organism. Evolution of intermediate levels of defenses may be adaptive in environments where both predators and competitors are present, although intermedi-
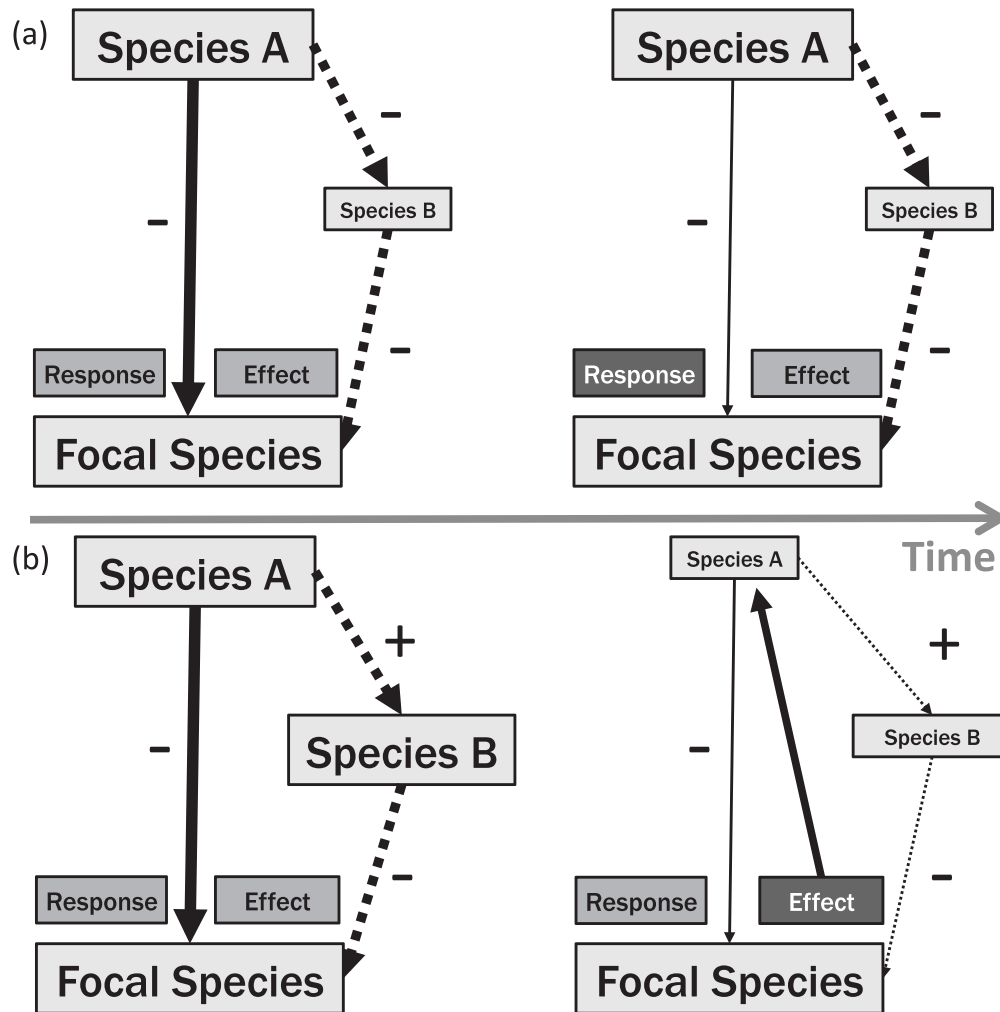
Figure 2: Hypothetical responses to indirect ecological effects depend on the nature of the direct (solid lines) and indirect (dotted lines) species interactions. In *a*, the indirect effect is positive and the focal species evolves increased response to species A (e.g., by increasing growth rate), thus reducing the negative effect of species A without affecting the abundance of A but maintaining the positive indirect effect mediated through species B. In *b*, the indirect effect is negative and the focal species evolves increased effect on species A (e.g., by avoiding consumption), thus reducing the abundance of A, which decreases the direct effect of A, but also the abundance of B, which decreases the indirect effect mediated through B. Adapted from Miller and Travis (1996). A color version of this figure is available online.

ate defense levels will be less adaptive to either predators or competitors in pairwise scenarios. In the next section, we further examine how indirect ecological effects may affect trait evolution (fig. 2).

Evolution in Response to Indirect Species Interactions

Ecologists have long recognized the importance of indirect ecological effects because their frequency and magnitude rival the importance of direct species interactions (Vandermeer 1969; Neill 1974; Miller and Kerfoot 1987; Strauss 1991; Menge 1995). An indirect ecological effect occurs when the interaction between two species is altered by the presence of other species (Strauss 1991). The additional species can alter pairwise interactions by either altering the density of other species or the traits of other species (Miller and Kerfoot 1987; Wootton 1994; Werner and Peacor 2003). Either of these mechanisms of indirect ecological effects can lead to changes in selection pressure on species traits (Inouye and Stinchcombe 2001; Walsh 2013; terHorst et al. 2015).

The optimal way for species to evolve in response to indirect ecological effects depends on the nature of both indirect and direct species interactions (Miller and Travis 1996). Species can evolve to alter their effects on other species (i.e., the extent to which they affect fitness of the other species) or their responses to other species (i.e., the extent to which

their own fitness is affected by other species; fig. 2). For example, plants may increase their effect on herbivores by evolving increased production of secondary metabolites that reduce consumption and decrease herbivore fitness (fig. 2). Alternatively, plants could increase their response to herbivores by evolving increased rates of leaf production, which could reduce the negative effects of herbivory on plant size, but maintain herbivore fitness. These effects and responses may or may not be governed by the same traits or genes. The optimal evolutionary pathway in response to indirect effects depends on the direction and magnitude of the direct interactions with other species (Miller and Travis 1996; fig. 2). For example, in a three-species system in which a focal prey species experiences negative effects from a predator and competitor but positive indirect effects because predators reduce competitor density, the focal species should increase its effect on other species because this will reduce negative direct effects while maintaining the positive indirect effect (fig. 2a). This early theory on evolution in response to indirect effects highlights the complexity of predicting evolutionary responses, even in relatively simple three-species communities (Walsh 2013).

There are an increasing number of examples of evolutionary change in traits in response to indirect ecological effects (Walsh 2013). In Trinidadian streams, predators reduce killifish densities, which indirectly increases resource availability to surviving killifish. The increase in resource availability alters the trajectory of killifish life-history evolution and drives traits in the opposite direction as the direct effect of predators (Walsh and Reznick 2008, 2010). Another example comes from populations of protozoa that live inside carnivorous pitcher plants. A focal protozoan species experienced selection for reduced cell size in response to direct effects of predators or competitors (terHorst et al. 2010a; terHorst 2011) but experienced selection in the opposite direction when both were present, thus negating the independent direct effects on the focal species (terHorst 2010). Mycorrhizal fungi decreased the biomass of snap beans, indirectly affecting the density of spider mites living on the plants; this indirect effect also altered the evolution of fecundity and time to maturity in the spider mites (Bonte et al. 2010). Future studies would benefit from identifying traits as either effect or response traits to determine whether the predictions of Miller and Travis (1996) hold in natural communities.

When indirect ecological effects occur, they may drive nonadditive selection (Strauss et al. 2005; Haloin and Strauss 2008; terHorst et al. 2015). Nonadditive selection occurs when the selection imposed by one species on another is altered by the presence of a third species (Strauss et al. 2005; terHorst et al. 2015; fig. 1). terHorst et al. (2015) described a framework for testing for nonadditive selection in manipulative experiments commonly used by community ecologists. Early work suggests that nonadditive selection in response to indirect ecological effects may be common in natural communities and similar in magnitude to selection in response to direct species interactions (terHorst et al. 2015). For example, Juenger and Bergelson (1998) found selection on flowering phenology in *Ipomopsis aggregata* in response to interactions with either flies or caterpillars; yet when both species were present, they found no selection on phenology. This may occur because of antagonistic interactions between flies and caterpillars or because of changes in plant chemistry that reduce damage that occur only when both herbivores are present (Juenger and Bergelson 1998). Lau (2008) demonstrated that insect herbivores imposed selection on plant resistance to herbivores but only when a competing invasive plant species was present, likely because the competitor attracted more herbivorous insects and indirectly affected plant fitness. Although there are a few such examples in the literature (Stinchcombe and Rausher 2001, 2002; Lankau and Strauss 2008; Lau 2008), more studies are needed to rigorously test the prevalence of nonadditive selection in natural communities (terHorst et al. 2015, 2017).

Evolutionary Genetics in a Community Context

To this point, we have discussed how a multispecies community context results in complex interactions among species, leading to a variety of selection pressures in different species assemblages. We now turn toward understanding the genetics within and among species and how these genetic architectures can alter responses to these forms of selection. Organisms are not the sum of their individual traits but are composed of an integrated, interacting, and interdependent web of genetic pathways that interact directly and indirectly to mediate the phenotypic expression of their traits. The genetic variation at the level of the population results in phenotypic variation for those traits among individuals.

Genetic Correlations among Traits within Species

Species are often under various selection pressures acting on multiple different traits. When any trait is under selection, correlations between traits affect the evolutionary responses of other traits. The evolutionary response of one trait depends on selection on that trait as well as selection on all correlated traits (fig. 3). For quantitative traits, the genetic variance-covariance matrix (the **G** matrix; Conner and Hartl 2004; Hine and Blows 2006) summarizes the relationships between multiple quantitative traits and thus their potential for evolutionary change. For example, partridge pea (*Chamaecrista fasciculata*) populations transplanted to locations mimicking future temperature regimes experienced direct selection for both increased leaf number and reproductive stage (later flowering). However, these two traits were
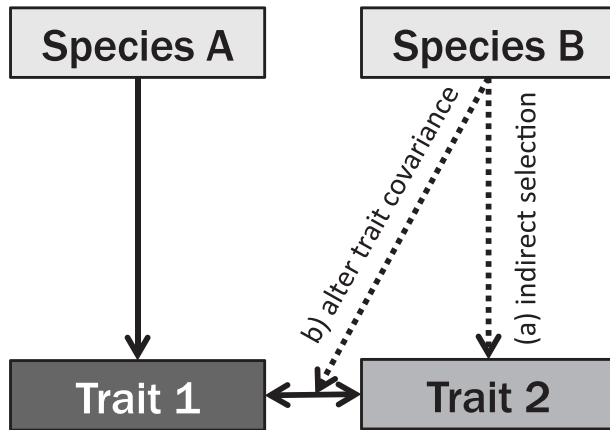
Figure 3: Evolution of a trait in a focal species in response to species A may be affected in various ways by the presence of species B because of genetic correlations among traits: B affects the evolution of trait 2, which is correlated with trait 1 (*a*), or B alters the genetic correlation between traits 1 and 2 (*b*). A color version of this figure is available online.

negatively genetically correlated (genotypes with more leaves tended to have earlier flowering; Etterson and Shaw 2001). This misalignment between the axis of genetic variation and the direction of selection represents an evolutionary constraint (Lau and terHorst 2015), in this case enough to severely limit plant adaptation to climate change. Further, the presence of multiple species can affect the expression of genetic variance in a trait or covariances among traits either by altering selection on traits or effective population size (Roff 2000); these changes alter the **G** matrix and thereby trait evolution (fig. 3). Evolution predicted from single-trait studies can substantially depart from what we might predict when we take multiple traits into account.

One way that genetic correlations can be important in a community context is when the traits that mediate the interactions of a focal species with one partner are genetically correlated with traits that mediate interactions with another partner. This concept is similar to ecological pleiotropy but at the genetic level. Strauss and Irwin (2004) define ecological pleiotropy as a single trait that affects interactions with multiple species. However, here we are describing the case of multiple covarying traits that affect interactions with multiple species acting as a single trait, in that they limit the capacity of each other to evolve. Our loosely defined scenario of ecological pleiotropy is likely common, given that shared biosynthetic pathways often contribute to traits underlying multiple species interactions (e.g., plant hormones and secondary chemistry influence pollinator attraction, defense against herbivory and infection, and allocation to belowground symbionts; Strauss and Irwin 2004; Berenbaum and Zangerl 2006). These genetic correlations

can facilitate or constrain evolution, at least in the short term, depending on the direction of selection imposed by various community members (Lau and terHorst 2015).

Genetic covariances can result from either linkage disequilibrium or pleiotropy (Falconer and Mackay 1996; Kopp and Matuszewski 2014), although they may be uncoupled via recombination, mutation, or other changes in allele frequencies that cause changes in the *G* matrix over time (Steppan et al. 2002; Arnold et al. 2008; Wood and Brodie 2015). To the extent that genetic correlations between two traits mediating species interactions are the result of genetic pleiotropy, the evolution of interactions with both species will be coupled, and thus the evolution of any single species interaction will depend on the community context. When linked traits govern interactions between predator and prey, those correlations affect coevolutionary stability and can lead to maladaptation of species to one another (Nuismer and Doebeli 2004). Experimental evolution approaches using the bacteria *Pseudomonas* and two antagonists (a virus and a predatory protist) demonstrated that community context influenced pairwise coevolution between bacteria and virus because of costs of defense against the predator (Friman and Buckling 2013; Friman et al. 2015). Similarly, genetic covariance between plant resistances to various herbivores on horse nettle (*Solanum carolinense*) constrained plant adaptation to the herbivore community (Wise and Rausher 2013).

Interestingly, pleiotropy governing two interactions does not always couple their evolution. Several plant genes are known to be involved in the signaling and establishment of symbiosis with both nitrogen-fixing rhizobia and arbuscular mycorrhizal fungi, leading geneticists to hypothesize a common symbiosis pathway in hosts. In this issue, Ossler and Heath (2018) used a quantitative genetic approach to test whether this pleiotropy results in genetic covariances between host traits but found little evidence for it, suggesting that trait variation exists at other loci. Thus, the evolutionary effects of pleiotropy in multispecies interactions will depend on whether the pleiotropic genes themselves actually harbor the genetic variation on which selection acts.

Coevolution of Traits in Different Species

In the examples above, selection acts on genetically correlated traits in a variable host, but genetic variation in the species imposing that selection was not considered. However, biotic agents of selection also evolve. From an evolutionary genetics perspective, coevolution occurs when genetic changes in one or more species mediate genetic changes in another (Thompson 2009). Here we adopt the perspective of Kiester et al. (1984) that coevolution occurs between traits in two or more species and not, strictly speaking, between species. Aspects of the environment are well known to alter selection (Kingsolver et al. 2001; Siepielski et al. 2009), and envi-

ronmentally dependent selection is described by genotype × environment interactions for fitness (usually an environmentally dependent regression of fitness on a trait). It follows, then, that genotype × genotype interactions among species (also called transgenomic or intergenomic epistasis) arise when the environment itself is another species and can thus evolve (Wolf 2000; Wade 2007; Heath 2010). This is best exemplified (but not limited to) the field of community genetics, in which the genotype of one species (e.g., a tree) affects the assemblage of associated species (e.g., insects, fungi, microbes). Changes in tree genotype frequencies are likely to alter selection on associated species. Indeed, genotype × genotype effects on fitness are, by definition, the driver of coevolutionary change (Parker 1995) because coevolution requires that evolution (genetic change) in one species precipitates evolution (genetic change) in another (Janzen 1980). Wade and Drown (2016) argue that intergenomic epistasis can result in trait correlations among species and result in the maintenance of species interactions.

In a community context, genotype × genotype interactions may be extended to higher orders. For example, genotype × genotype × environment interactions represent environmentally variable coevolutionary selection (e.g., if direction or magnitude of the effects of species B in fig. 3 were dependent on environmental context) or selection mosaics (Gomulkiewicz et al. 2007; Thompson 2009). Genotype × genotype × genotype interactions represent three-species transgenomic epistasis. We could extend this concept ad infinitum, at least theoretically, although the number of experimental treatments, possible diminishing effect sizes, and decreased statistical power mean these effects quickly become difficult to detect. The extent to which these higher-order effects can be explored will depend on replication in experiments, which may be more easily explored in microbial or microcosm-based communities. Nevertheless, genetic changes that occur within a species can have cascading effects on selection imposed on the other species in the community, if these genetic changes alter the relationship between traits and fitness.

Eco-Evolutionary Feedbacks

The past 2 decades of research in evolutionary ecology have led to an increased realization that organisms can evolve on ecological timescales (reviewed in Thompson 1998; Fussmann et al. 2007; Johnson and Stinchcombe 2007; Schoener 2011). This is especially true of short-lived species with short generation times but can also apply to longer-lived species that experience strong selection pressure (Reznick and Ghalambor 2001; Visser 2008; Lavergne et al. 2010; Moran and Alexander 2014; Colautti and Lau 2015). In terms of evolution in a community context, this suggests that the complex ecological interactions that impose selection may not be consistent over time. As species evolve in

response to multiple interactions in a community context, such evolution may indirectly affect the magnitude or direction of interactions with other species (Yoshida et al. 2003; terHorst et al. 2010b), population demography (Reznick et al. 2012), species diversity (Schreiber et al. 2011), community assembly (Pantel et al. 2015; terHorst and Zee 2016), or ecosystem function (Bassar et al. 2010; terHorst et al. 2014), all of which may also feed back to further alter evolutionary trajectories (fig. 4). Indirect effects between ecological and evolutionary processes result in eco-evolutionary feedbacks that may be critical for understanding evolution in a community context as well as long-term evolutionary outcomes.

Eco-Evo Feedbacks Facilitate Coexistence

There is mounting empirical and theoretical evidence that eco-evolutionary feedbacks can play a role in mediating species coexistence and maintaining genetic polymorphisms (Lankau and Strauss 2007; Schreiber et al. 2011; Vasseur et al. 2011; Ellner 2013; Hiltunen et al. 2013; Patel and Schreiber 2015; Klauschies et al. 2016; Schreiber et al. 2018). The maintenance of this diversity occurs via a community-level Red Queen dynamic, in which the frequencies of the different species and genotypes are constantly shifting in response to one another (Klauschies et al. 2016). For example, Lankau and Strauss (2007) studied eco-evolutionary feedbacks in plant communities, including multiple genotypes of *Brassica nigra* that produce varying levels of an allelochemical (sinigrin) that kills mycorrhizal fungi that are beneficial to other plant species. This plant community engages in an eco-evolutionary rock-paper-scissors dynamic, in which *B. nigra* genotypes with high sinigrin concentrations increase in frequency when other plant species are common. After the high sinigrin genotypes outcompete other species and become common, low sinigrin *B. nigra* genotypes that were previously unable to invade replace high sinigrin *B. nigra* genotypes, because producing sinigrin is expensive and decreases intraspecific competitive ability. As the low sinigrin genotypes become common, other plant species increase in frequency, starting the cycle over again.

In chemostat experiments with algae, flagellates, and rotifers, Hiltunen et al. (2013) found a similar Red Queen dynamic. In this intraguild predation system (Polis and Holt 1992), the flagellates are the intraguild prey, the rotifers are the intraguild predator, and the algae (the common prey) are evolving. Consistent with model predictions, Hiltunen et al. (2013) found eco-evolutionary cycling as the algae evolved greater defense against the more abundant predator (losing defense against the less abundant predator). Theoretical work shows that a similar dynamic arises when it is the intraguild predator evolving to specialize on the more common prey species (Patel and Schreiber 2015). More complex cycles involving shifts between more
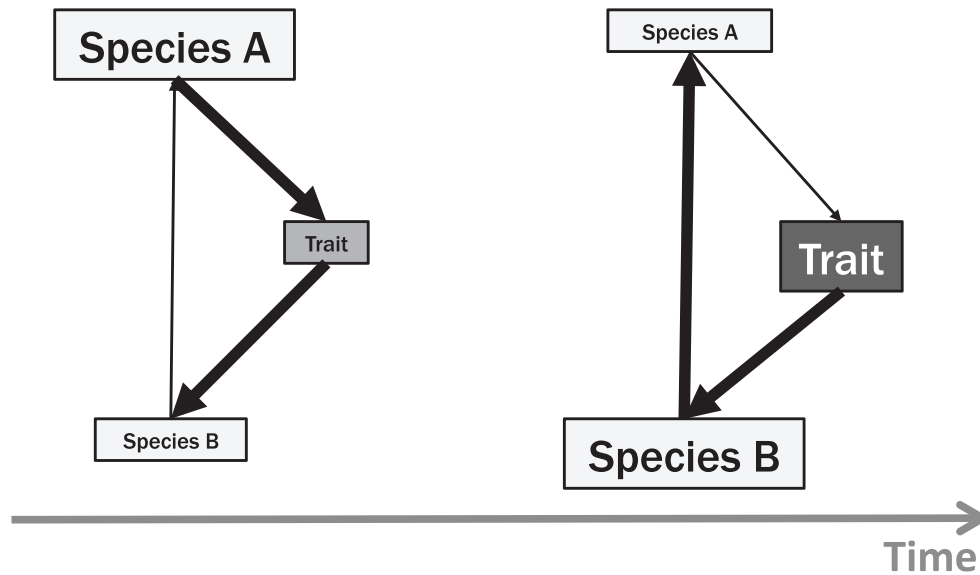
Figure 4: Eco-evo feedbacks occur when one species (A) alters trait evolution in another species (B), which then feeds back to affect species A. Such feedbacks could potentially occur indefinitely. A color version of this figure is available online.

eco-evolutionary community states are observed in models where species evolve defenses against multiple predators or evolve resource use of multiple prey (Schreiber et al. 2018). To what extent these eco-evolutionary cycles are common in nature remains to be seen.

Effects of Evolution on Community Diversity and Stability

At the heart of considering evolution in a community context is determining how the complex networks of species interactions in a community affect the evolutionary response of each species in the community. However, we must also consider how evolution of any species affects the network itself through eco-evolutionary feedbacks. Theoretical work has asked how eco-evolutionary feedbacks affect persistence and diversity in food webs composed of many competing species (terHorst et al. 2010*b*). Kondoh (2003) found that behavioral shifts in prey preferences could lead to a positive relationship between food web complexity and diversity. In contrast, when prey preferences evolved because of changes in allele frequencies, Yamaguchi et al. (2011) did not find a positive relationship between complexity and diversity, even at high mutation rates. However, high rates of evolution coupled with high network connectance increased community stability when compared with nonevolving communities. For communities with lower connectance, evolution (whether rapid or slow) led to more extinctions than in nonevolving communities.

The latter finding that evolution increases network stability is consistent with two recent theoretical studies. Barabas

and D'Andrea (2016) simulated multiple competing species to show that intraspecific variation and evolution increased community stability. In this issue, Patel et al. (2018) show that eco-evo feedbacks can stabilize otherwise unstable communities and vice versa, but the outcome depends on genetic correlations between traits and the rate of evolution relative to ecological processes. Together, these studies suggest that evolution on ecological timescales can alter community stability.

Genetic Architecture Affects Eco-Evo Feedbacks

Evolutionary theory has shown that genetic architecture can affect the response of a single species to selection, including whether selection will drive species phenotypes to a fitness optimum and how efficiently it will get there (Lewontin and Kojima 1960; Lande 1979; Otto and Gerstein 2008; Kopp and Matuszewski 2014). These effects of genetic architecture can have cascading effects on community processes, species persistence, and the strength of eco-evolutionary feedbacks. In a pairwise coevolutionary predator-prey dynamic, increasing the number of loci that determine an ecologically important phenotype can dampen or stabilize predator-prey cycles (Doebeli 1997). If predators evolve at fewer loci than prey, then this increases stability (Yamamichi and Ellner 2016). In this issue, Patel et al. (2018) discuss how genetic architecture affects community and evolutionary stability in eco-evo feedback scenarios. Schreiber et al. (2018) demonstrated that the genetic architecture of a species evolving in response to two other species affects the

strength and direction of the eco-evolutionary feedback. Synergistic pleiotropy, in which pleiotropic effects enhance fitness, facilitates coexistence while antagonistic pleiotropy disrupts coexistence (Schreiber et al. 2018). Diploidy, by slowing down the rate at which alleles are lost, can mediate coexistence through an eco-evolutionary storage effect; this storage effect occurs when alleles that are not currently adaptive are retained as hidden alleles in heterozygotes but may prove to be adaptive as the community composition changes because of the eco-evolutionary dynamics (Schreiber et al. 2018). Such a storage effect is not possible in haploid populations, but haploids may respond more immediately to multispecies eco-evolutionary dynamics (Otto and Gerstein 2008). Continued exploration of how eco-evolutionary feedbacks interact with evolutionary genetics or syngenomics is an avenue of research that is ripe for future exploration.

Empirical Examples of Eco-Evo Feedbacks

Empirical examples of eco-evolutionary feedbacks have begun to accumulate over the past few years. For example, rapid evolution of two life-history traits (shorter life span and later flowering time) in common evening primrose led to increased resistance to a specialist seed predator, which then reduced the density of the seed predator, presumably leading to weaker selection on those traits (Agrawal et al. 2012). In a more complex community, how Trinidadian guppies evolved in response to predators and prey affected the primary productivity and community structure of the benthic community, which likely feeds back to change the selection pressure on guppies (Palkovacs et al. 2009; Bassar et al. 2010). Others have demonstrated similar eco-evolutionary feedbacks in communities of plants and aphids (Turcotte et al. 2013), sticklebacks (Harmon et al. 2009; Matthews et al. 2016; Rudman and Schluter 2016), alewives (Post et al. 2008; Palkovacs and Post 2009), and frugivorous birds and trees (Galetti et al. 2013). These conceptual and empirical insights into eco-evolutionary feedbacks emphasize the potential for these processes to have persistent effects on trait evolution and the structure and diversity of ecological communities.

Future Directions

Here we have highlighted a few aspects of what is important for understanding evolution in a community context. The remaining papers in this issue provide deeper insight into these topics. Generally, it remains unclear under which circumstances it is critical to consider a community context to predict the evolutionary trajectory of one trait in one species. How much variation in trait evolution can be explained by pairwise interactions, by multiple species interactions, by indirect ecological effects, by ecological pleiotropy, or by genetic correlations? What community patterns result from multispecies evolution that differ from those predicted from only an understanding of pairwise species evolution? Does the community context affect some trophic levels more than others? What factors affect the relative importance of pairwise versus community context among systems? Because of the many avenues of research in this field that deserve further attention from both theoretical and empirical perspectives, it is difficult to evaluate the relative importance of evolution in a community context. Although we are approaching the ability to answer a few of these questions in a few limited systems (terHorst et al. 2015), more research across this field is required to make any generalizations across space and time.

In particular, we advocate the need to further understand how genetic architecture influences evolutionary responses in different species and the extent to which this can affect eco-evolutionary feedbacks. Much of the theory to this point has used a quantitative genetics framework or a single locus (but see Doebeli 1997; Yamaguchi et al. 2011; Schreiber et al. 2018). There are still many open questions of how multilocus traits affect evolutionary responses and eco-evolutionary feedbacks within a community. Do more complex genetics change the conditions for coexistence or the predicted evolutionary response in a community context? Do different genetic architectures at different trophic levels alter the outcome of eco-evolutionary feedbacks (Yamamichi and Ellner 2016)?

Understanding evolution in a community context may be important for fundamental questions in ecology, such as the relationships among diversity, stability, and ecosystem function. Moreover, the concept of evolution in a community context should be applied across more disciplines than just ecology and evolutionary biology. For example, a better understanding of evolution in diverse microbial communities associated with agriculture could lead to increased crop production or, more importantly, lower chemical inputs to achieve the same production. Incorporating a community context into evolutionary medicine may increase our ability to understand the evolution of resistance in infectious bacteria and viruses or how hosts (human or other species) respond to multiple infections by parasites (Ewald 2004, 2013).

As with all theoretical work, theory on evolution in a community context that incorporates more realistic assumptions will also move us toward greater understanding of evolutionary dynamics in complex communities. Work that incorporates more interactions among species and their coevolving traits is needed but also requires understanding even more complex dynamics. Determining how more ecological factors (density, species diversity) interact with more evolutionary factors (genetic variation, selection) will move forward our understanding of eco-evo feedbacks. For example, genetic

variation is required for evolution to occur, and population density plays a strong role in regulating populations, but density may also affect the extent of genetic variation in a population.

Theory on evolution in a community context has outpaced the testing of that theory with experiments. This is understandable, given the complexity and time needed to conduct evolutionary experiments in multispecies systems. We must give thought to how to test such theory. Microbial systems have proven useful for testing theory in the laboratory because of their rapid ecological and evolutionary dynamics, but can the genetics of asexual haploids explain dynamics in macroorganisms that have historically received greater attention? Research need not be limited to microbial systems though; space for time substitutions could be used to estimate evolutionary changes in communities with different levels of species diversity.

As we emphasized earlier, the topics covered here are only a subset of topics related to evolution in a community context that are most related to other papers in this issue. We have neglected to cover many other topics that deserve further attention. For example, we have ignored spatial heterogeneity and variation in spatial structure that are likely to affect evolution in a community context in metacommunities (Nosil and Crespi 2004; Urban et al. 2008; Urban 2011). We have not discussed the importance of network connectance in communities, which is likely to affect the relative importance of evolution in a community context (Leibold et al. 2005). Demography may also be critical; ontogenetic shifts in species interactions will affect the relative importance of selection on different life stages (Williamson et al. 2004; Gagliano et al. 2007). Although there has been some work on these topics, they deserve further attention to understand evolution in a community context.

Acknowledgments

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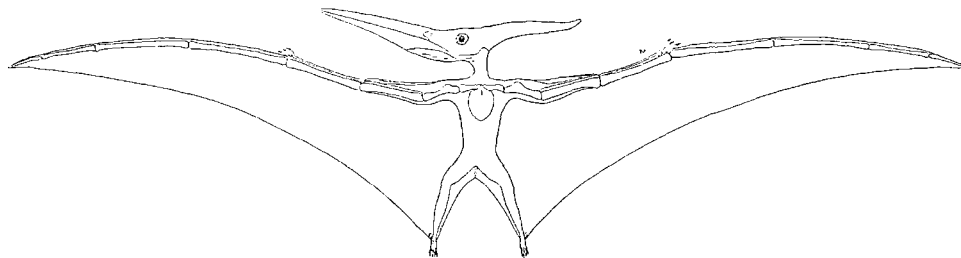
Pteranodon "is from the Kansas Chalk, a creature with an alar expanse of eighteen feet! Vast in comparison with the diminutive body. In Pteranodon the tail is reduced to a vestige which afforded but little support to the interfemoral membrane." From "Volant Adaptation in Vertebrates" by Richard S. Lull (*The American Naturalist*, 1906, 40:537–566).