

Intraspecific Genetic Variation and Species Interactions Contribute to Community Evolution

Thomas G. Whitham, Gerard J. Allan,
Hillary F. Cooper, and Stephen M. Shuster

Department of Biological Sciences and Center for Adaptable Western Landscapes, Northern
Arizona University, Flagstaff, Arizona 86011, USA; email: Thomas.Whitham@nau.edu

Annu. Rev. Ecol. Evol. Syst. 2020. 51:587–612

First published as a Review in Advance on
September 4, 2020

The *Annual Review of Ecology, Evolution, and
Systematics* is online at ecolsys.annualreviews.org

<https://doi.org/10.1146/annurev-ecolsys-011720-123655>

Copyright © 2020 by Annual Reviews.
All rights reserved

Keywords

community heritability, community genetic correlations, community
phenotype, interspecific indirect genetic effects, community selection and
evolution, multilevel selection

Abstract

Evolution has been viewed as occurring primarily through selection among individuals. We present a framework based on multilevel selection for evaluating evolutionary change from individuals to communities, with supporting empirical evidence. Essential to this evaluation is the role that interspecific indirect genetic effects play in shaping community organization, in generating variation among community phenotypes, and in creating community heritability. If communities vary in phenotype, and those phenotypes are heritable and subject to selection at multiple levels, then a community view of evolution must be merged with mainstream evolutionary theory. Rapid environmental change during the Anthropocene will require a better understanding of these evolutionary processes, especially selection acting at the community level, which has the potential to eliminate whole communities while favoring others.

ANNUAL REVIEWS CONNECT

www.annualreviews.org

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Individual selection:
differential survival and/or proliferation of individuals

Community:
an association of interacting species that lives in a particular area; not to be confused with an assemblage of species that does not necessarily require interspecific indirect genetic effects (IIGEs) that have fitness consequences

Coevolution:
reciprocal evolutionary change in interacting species

Diffuse coevolution:
the evolutionary responses of individual species to complexes of species with which they are interacting

Neutral theory:
population and community change arise only through ecological drift, stochastic but limited dispersal, and random speciation, and all individuals within a trophic level have the same chances of reproduction and death regardless of the species identity; neutrality is defined as per capita ecological equivalence among all individuals of every species in a given trophically defined community

1. INTRODUCTION

Williams (1966, p. 5) asserted that selection acts most effectively, if not exclusively, at the individual level. He argued that “[i]n explaining adaptation, one should assume the adequacy of the simplest form of natural selection, that of alternative alleles in Mendelian populations, unless the evidence clearly shows that this theory does not suffice.” Williams’s thesis was greeted with certainty by most behavioral, ecological, and evolutionary biologists, a consensus that largely persists today. Individual selection theory was also widely accepted in studies of community organization. Trait evolution in considerations of pairwise or multispecies interactions (e.g., coevolution, diffuse coevolution, evolutionary hot and cold spots; Ehrlich & Raven 1964, Janzen 1980, Levin et al. 1990, Thompson 1994) is explained in terms of selection acting on individuals via interactions imposed by individuals of other species. Selection acting at the individual level also allows ecological communities to be viewed as assemblages of interchangeable units, in the sense that either they represent random associations of populations (i.e., neutral theory; Hubbell 2001) or individual species are functionally equivalent in how they contribute to ecosystem function (Hubbell 2005). These species may sort themselves into operationally indistinguishable units in which local communities have little to contribute to our understanding of ecology and evolution (Ricklefs 2008). Indeed, most biologists accept that selection occurs only at the individual level and that no components of fitness exist at higher levels (but see Sections 2.2 and 2.3 on group selection and community selection, respectively).

We argue that to understand the evolution of complex communities it is necessary to invoke the existence of a more elaborate system by which phenotypes are expressed, the ways in which genetic elements are transmitted, how fitness is measured, and how each of these elements changes over time. This greater complexity is supported by agricultural literature (Robertson 1957, Griffing 1967, Falconer & McKay 1996, Simmonds 1996, Wade et al. 2010) and by empirical studies of group and higher levels of selection by Wade (1977, 2016), Wilson (1975, 1983), and Goodnight (1990a,b; 1995; 2000), which have expanded into the field of community genetics (Antonovics 1992). This combined framework has led to studies of the genetic interactions that occur within and among species to yield complex communities (e.g., Whitham et al. 2003, 2006, 2008; Neuhauser et al. 2003; Shuster et al. 2006; Allan et al. 2012; Crutsinger 2016; Weber et al. 2017; terHorst et al. 2018).

The distinctions among these alternative hypotheses of community organization (random associations of populations, assemblages of interchangeable units, or genetically interconnected complex communities) are important for both basic and applied reasons. Knowing how communities are organized is fundamental to understanding the principles of community assembly and evolution, which in turn greatly affects their management, especially in times of great challenges such as climate change. **Figure 1** shows an increasingly common example of stand-level habitat loss due to record drought (Williams et al. 2020). Using this example, we ask whether selection operates on individual trees, groups of conspecific trees, whole communities, or all three levels simultaneously. The community and ecosystem consequences of this disturbance depend on the levels of selection involved and the genetics-based linkages among the many species that, in turn, depend on this critical habitat type for their survival. For example, if communities are assemblages of interchangeable units, then the loss of one species is unlikely to cascade to affect whole communities and ecosystems. In contrast, if communities consist of genetically linked assemblages of interacting species, then losses of individual species, especially highly interactive species, are likely to have much greater consequences for biodiversity and ecosystem stability. Here we experimentally examine these possibilities.

A key distinction between community and population genetics is that “community genetics revolutionizes the way genes are functionally annotated, because the genes that cause a phenotype in



Figure 1

Remains of a gallery riparian forest that was decimated by the megadrought in which most trees and shrubs died due to declining stream flows and water table. Tree ring analyses indicate that the period 2000–2018 in the American Southwest was the second-worst drought in 1,200 years (Williams et al. 2020). The opportunity for selection during such events can be very high and may operate at individual, group, and community levels across this landscape. This forest provides critical habitat for many rare, sensitive, and endangered species (LCR MSCP 2004). (a) Overview of the Bill Williams National Wildlife Refuge, Arizona, USA. (b) Inside view of a stand. Photo in panel a by Hillary Cooper, 2017 (public domain), reproduced from Whitham et al. (2020). Photo in panel b by Tom Whitham, 2017.

one species can reside in the genome of another” (Wade 2007, p. 186). Gilbert et al. (2012) extend this perspective, asserting that the individual is a conceptual fallacy because plants and animals intimately interact with symbiotic microorganisms that are essential to their survival. This view suggests that because classical population genetics does not consider multispecies complexity, a community genetics approach is necessary for understanding how selection influences the composition, structure, and evolution of communities. Statistical methods now exist for partitioning the evolutionary effects of selection at multiple levels (Goodnight et al. 1992; Wade 1977, 1978, 2016).

Community genetics, like other multilevel selection frameworks, assumes that selection acts simultaneously at molecular, genetic, individual, family, group, and higher levels of organization (Wade 1985, Stevens et al. 1995, Wilson 1997, Whitham et al. 2003). Multilevel selection occurs when relative fitness depends on the phenotype of the individual, as well as on the phenotypes of the group(s) to which individuals belong (e.g., a plant–pollinator community or a plant–mycorrhizal fungal community). Here we evaluate the concept of community evolution, which we define as the outcome of selection operating at multiple levels that results in the differential survival and proliferation of communities. Thus, community evolution can be detected as a change in the average community phenotype (i.e., the richness and abundance of species associated with an individual organism; Whitham et al. 2003) through time. This concept differs from some uses of the phrase “evolution in a community context” (cf. Rausher 1996, Strauss & Irwin 2004, Weber et al. 2017, terHorst et al. 2018), which is based on individual-level selection, does not involve multilevel selection, and is more equivalent to coevolution and diffuse evolution that operate at lower levels (Levin et al. 1990, Thompson 1994; see **Supplemental Appendix 1**).

Group selection:

covariance between group phenotype and group fitness allows certain group phenotypes to propagate in disproportionate numbers

Community selection:

differential survival and/or reproduction of communities

Community genetics:

the study of the genetic interactions that occur among species and their abiotic environment in complex communities

Multilevel selection:

selection that occurs when relative fitness depends on the properties of individuals, as well as on the properties of the group(s) to which individuals belong

Community

evolution: the outcome of selection operating at multiple levels that results in the differential survival and proliferation of communities and can be detected as a change in the average community phenotype in response to a selection event through time

Community

phenotype: the richness and abundance of species associated with an individual host organism that result from IIGEs; these can be summarized using multivariate statistics as a univariate trait that can be analyzed as a quantitative trait

Evolution in a

community context:

evolution that occurs in response to more than one species

Our emphasis on multilevel selection also separates our discussion from considerations of holobiont and associated hologenome theory (Zilber-Rosenberg & Rosenberg 2008), as well as from its critics (Foster et al. 2017). This theory emphasizes the holobiome, usually a multicellular host and its microbial symbionts, as the primary unit of selection (Bordenstein & Theis 2015), whereas critics emphasize difficulties associated with the resolution of conflict between individual- and higher-level selection, or the possibility that symbionts have evolutionary trajectories independent of their hosts (Moran & Sloan 2015, Douglas & Werren 2016). When selection is presumed at the outset to occur on multiple levels of biological organization, this debate is no longer relevant because multilevel selection makes no a priori assumptions about the preeminence of one level of selection over another, or the necessity that members of a community evolve as a unit (Wade 2016, Roughgarden et al. 2017).

While individual and community approaches may appear to be mutually exclusive, evolutionary biologists have begun to consider that individual, group, and higher levels of selection exist as a continuum. For organisms with few interactions with other species, classic ecology and population genetics may suffice, but for other organisms with many complex interactions (e.g., species of large community effects, such as a long-lived tree, a pathogen, or an invasive annual grass, that affect associated communities), multilevel selection may be needed to understand the evolutionary process. Here, following a well-established causal framework (Darwin 1859, Lewontin 1970, Lande & Arnold 1983, Falconer & McKay 1996, Wade 2016), we consider evolutionary change at any organizational level as requiring three elements: (a) variation in phenotype among units, (b) heritability underlying unit phenotypes, and (c) selection acting among unit phenotypes, that is, the differential survival and/or proliferation of units on the basis of phenotypic differences. Note that phenotypic variation and heritability are considered separately because the existence of phenotypic variation does not mean that it is heritable, which must be demonstrated. We expand upon this conceptual framework to illustrate how these processes may simultaneously operate at individual, group, and community levels of organization, and we provide evidence of these processes on the basis of experimental studies suggesting that intraspecific genetic variation and species interactions contribute to community evolution. This framework provides testable hypotheses for establishing the relative importance of each of these elements and how they contribute to evolutionary change at each level of organization, allowing researchers to focus on the appropriate levels for their particular system. The next section provides the theoretical framework for understanding multilevel selection, and the subsequent sections present empirical examples of how multilevel selection is manifested in natural complex communities.

2. THE ELEMENTS OF EVOLUTIONARY CHANGE

2.1. Individuals

For evolution to occur at the individual level, variation must occur among individual phenotypes, heritability must exist such that progeny inherit their parents' traits, and selection upon individuals must ensue whereby a covariance between individual phenotype and individual relative fitness allows certain phenotypes to propagate in disproportionate numbers.

2.1.1. Variation. Phenotypic variation among individuals within populations arises from variation in individual genotype, the environment in which those individuals are reared, the interactions between genotype and environment, and the interactions among individual phenotypes within the population that affect phenotypic expression.

2.1.2. Heritability. The inheritance of individual traits depends on genetic factors that underlie phenotypic resemblance among related individuals (Falconer & McKay 1996). Heritability in the broad sense, H^2 , equals the proportion of total phenotypic variation, V_P , that is due to variation in genetic factors, V_G . Thus, $H^2 = V_G/V_P$, where $V_P = V_G + V_E$ and V_E equals variation in environmental influences on phenotype (assuming no gene–environment interactions, although this and other genetic interactions can make additive effects context dependent). Heritability in the narrow sense, b^2 , equals the proportion of total genetic variation influencing a trait, V_G , that is capable of producing a lasting response to selection. The latter component of variation is the additive genetic variance underlying phenotypic traits, or V_A . Thus, $b^2 = V_A/V_P$.

2.1.3. Selection. Differential survival and/or proliferation of individuals is most readily described by estimating the opportunity for selection, which, as Crow (1958) showed, compares the average fitness of the entire population with that of the breeding parents, and simplifies to the more familiar ratio of the variance in fitness to its squared average ($V_W/W^2 = I$). I measures the variance in relative fitness or the maximum change in phenotype that is possible due to a single episode of selection. When traits affecting fitness can be identified, selection can be defined as a covariance between phenotype and relative fitness, $\text{Cov}[z_{ijk}, w_{ijk}]$ (Price 1972), where z equals phenotype, w equals the relative fitness, and the subscript ijk identifies the value for the k th individual bearing the j th phenotype in the i th population. Like hierarchical components of variance, this covariance can be partitioned within and among the levels of biological organization at which selection occurs. Relative fitness can be defined in terms of performance, but survivorship and reproduction provide direct fitness measures. Relative fitness, w , equals absolute fitness, a_i , divided by the average fitness of all individuals in the population, W , or $w = a_i/W$.

2.2. Groups of Conspecific Individuals

For evolution to occur at the group level, variation must occur in average group phenotype, heritability must exist such that progeny groups inherit their parent groups' traits, and selection must ensue whereby a covariance between group phenotype and group fitness allows certain group phenotypes to propagate in disproportionate numbers. We include group selection because, despite persistent skepticism, group components of variation, heritability, and fitness are now increasingly recognized within multilevel selection models (Wade 2016). However, because we do not specifically consider these elements of group selection within our empirical community studies, we develop the conceptual framework for this section in **Supplemental Appendix 2**.

2.3. Communities of Interacting Species

For evolution to occur at the community level, variation must occur among community phenotypes (V_{ZC}), heritability must exist such that progeny communities inherit their parent communities' traits (H^2_C), and selection among communities must ensue whereby a covariance between community phenotype, Z_C , and community fitness, w_C ($= \text{Cov}[Z_C, w_C]$), allows differential survival and reproduction of certain community phenotypes, resulting in community evolution. Note that these definitions represent parameters specific to community-level processes and organization (see also **Supplemental Appendix 2**). They do not simply represent the sum or average of individual components of phenotypic variation, heritability, and selection, as explained below.

2.3.1. Variation. Consistent with multilevel selection frameworks (Whitham et al. 2003), all factors that influence variation at the individual and group levels described above contribute to

Broad sense: refers to clonal heritability, or the contribution of all genetic factors (additive, dominant, epistatic) to the total variance in phenotype; H^2 is the broad-sense heritability of a traditional phenotype, and H^2_C is the broad-sense heritability of a community or ecosystem phenotype

Narrow sense: refers to sexual reproduction; b^2 equals the proportion of total phenotypic variation influencing a trait that has lasting response to selection in sexually reproducing organisms (includes additive genetic variation)

Supplemental Material >

Interspecific indirect genetic effects (IIGEs)

interactions among individuals in one species that affect trait expression and fitness in another species; note that IIGEs are different than indirect genetic effects (IGEs) that are restricted to interactions among conspecific individuals

Community genetic correlations

changes in the composition of one community among plant genotypes that are mirrored by changes in the composition of another community

phenotypic variation at the community level. Within communities, genetics-based interactions among individuals in one species can be responsible for changes in the expression of traits in other associated species (cf. Wade 2007). These interspecific indirect genetic effects (IIGEs) occur because genetic variation underlying functional traits in a host species can influence the tendency for individual genotypes in other species to associate actively with that host or to avoid that host altogether. Such variation in the fitness of individuals in associated species causes selection to occur within a community context (cf. Shuster et al. 2006, Allan et al. 2012) and leads to differences in the numbers of individuals in different species that associate with particular host genotypes.

Although the influence of host genotype on community phenotype is clear, few studies have explored genetic variation or trait expression within associated species. However, some studies provide direct evidence that IIGEs drive particular host-symbiont associations. For example, Evans et al. (2008) showed strong genetic differentiation among mite populations found on cottonwoods; reciprocal transfer experiments confirmed that distinct mite lineages perform best on their natal host genotype (see reviews by Mopper 1996 and Mopper et al. 2000). Gehring et al. (2017) showed that mycorrhizal taxa associated with drought-tolerant and drought-resistant *Pinus edulis* host trees belong to different fungal phyla. Lamit et al. (2015a) showed consistent and strong community genetic correlations between canopy arthropod and leaf pathogen communities associated with individual cottonwood genotypes. More than 60 studies reviewed by Whitham et al. (2012) provide a critical test of the IIGE hypothesis (Shuster et al. 2006). Specifically, an observed, significant association of particular arthropod communities with individual plant genotypes provides evidence that selection within a community context has occurred and that there was a strong genetic component to community structure.

When the genotype of one species affects the fitness of another species but not the reverse, the IIGE is unidirectional. Such interactions appear to occur when community members are associated with long-lived hosts such as lichens on trees (Lamit et al. 2015b). These relationships are analogous to any other phenotype associated with the host organism (Johnson & Stinchcombe 2007). When the genotype of one species affects fitness and causes an associated change in the genotypic frequency of another species, which in turn causes a change in fitness for the first species (e.g., plant-mycorrhizal associations; Gehring et al. 2017), the IIGE is reciprocal. Such interactions are more difficult to study because they are dynamic, but they more readily increase the among-community component of the total variance in community phenotype compared with unidirectional interactions.

Phenotypic plasticity in functional traits of organisms (e.g., plant phenology; Cooper et al. 2019) has the potential to affect community phenotypes due to environmental change and subsequent changes in species interactions among community members (Fordyce 2006). While some community phenotypes are remarkably constant with environmental change (Keith et al. 2010), others are more plastic (Stone et al. 2018). Thus, phenotypic plasticity in one or more organisms within a community can create variation in community phenotypes.

Whereas descriptions of individual- and group-level variation can be understood by partitioning the components of phenotypic variance arising at the individual and group levels (see **Supplemental Appendix 2**), community phenotypes must instead be quantified in terms of the abundances of each species that constitutes the community. This approach links community genetics concepts with quantitative genetics methodology. Quantitative genetics allows the cumulative influences of alleles of small effect to be summarized as a normally distributed quantitative trait. In an analogous way, Whitham et al. (2003, 2006, 2012) have shown that the abundances of species comprising communities on different genotypes of trees can be summarized with nonmetric multidimensional scaling (NMDS) ordinations using the Bray-Curtis measure for dissimilarity among pairs of community samples (Faith et al. 1987, Minchin 1987, Clarke

Supplemental Material >

1993). One-way analysis of variance (ANOVA) of univariate NMDS scores grouped by host tree genotype captures the details of community organization as they are reflected in phenotypic covariance among communities associated with genetically related host organisms (Shuster et al. 2006, Whitham et al. 2006). We do not discuss the mechanisms of gene expression and interaction in this review, but this is not necessary for the inheritance of the community-level trait to be understood. Additional statistical methods for documenting species and community coassociations exist (Lamit et al. 2015a, Lau et al. 2016).

2.3.2. Heritability. Goodnight (1990a,b, 2000; see also Williams & Lenton 2007) notes that when interspecific interactions occur, genetically correlated traits between species are likely to arise, allowing a lasting response to community-level selection in a way that does not exist when selection acts on individuals alone. Goodnight (1990a, p. 1615) states that “if the interactions among the members of the community are passed intact from the ‘parent’ community to the ‘offspring’ community the interaction will be heritable at the community level” (see also Goodnight & Craig 1996).

Estimates of broad-sense community heritability, H^2_C (Shuster et al. 2006, Whitham et al. 2006), make use of the same statistical tools described above for documenting variation in community phenotype, but these results are used in a novel way to document heritability at the community level. To document community phenotype, NMDS provides a multivariate summary of the numbers of associated species present on genetically distinct host plants. This same statistical procedure collapses this variation into a unidimensional score that can be analyzed using standard methods for estimating the heritability of quantitative traits (Falconer & McKay 1996). ANOVA of the univariate NMDS scores of species abundances on host tree clones, grown in a common garden and grouped by genotype, identifies the fraction of total genetic variance influencing the composition of ecological communities that are associated with particular host organisms. This approach is identical to methods for identifying the broad-sense heritability of quantitative traits (H^2) (Becker 1985, Lynch & Walsh 1998). However, community heritability, H^2_C , is defined as “the contribution of all genetic factors influencing community phenotypic variation: $H^2_C = \sigma^2_{\text{among genotype}} / \sigma^2_{\text{total}}$ ” (Shuster et al. 2006, p. 993). This definition is appropriate because all plant genotypes with their associated communities were represented by multiple clones planted at random in common gardens (Whitham et al. 2003, 2006). Estimates of H^2_C also summarize the fitness consequences of genetically based interactions among individuals in different species as a result of selection acting within a community context; thus, H^2_C captures the “among-community fraction of the genetic variance affecting coevolving traits” (sensu Goodnight & Craig 1996). Note that this use of the term coevolving is not confined to descriptions of the evolutionary trajectories of pairs or even groups of species (sensu Ehrlich & Raven 1964) but rather refers more generally to how trait expression in one species influences trait expression and thus fitness in another species, that is, to IIGEs. Shuster et al. (2006, p. 993) further noted that “in addition to providing a means for documenting the existence of IIGEs among species within communities, estimates of H^2_C provide a statistical estimate of the phenotypic covariance of communities on groups of related host organisms.” Stated differently, within estimates of H^2_C , the observational components of community resemblance and the causal components of genetic variance within and among communities are equivalent.

2.3.3. Selection. Whitham et al. (2003; after Price 1972, Goodnight et al. 1992) considered multilevel selection by letting individual relative fitness, w , equal the combined effects of individual, group, and community components (i.e., multilevel selection). Here, the relative magnitude and sign of selection acting at individual, group, and community levels were identified by the partial regressions of relative fitness on individual, group, or community phenotype, respectively,

Community heritability: the tendency of related individuals to support similar communities and ecosystem processes or the phenotypic covariance of communities on genetically related host species; the corollary is that distantly related individuals will support more dissimilar communities

Opportunity for community selection:

a quantitative assessment of the variance in the relative fitness of communities; when measured in terms of the extinction and proliferation of foundation species individuals, $I_{\text{community}}$ equals the variance in community fitness divided by its squared average, or

$$V_{W \text{ community}} / W^2_{\text{community}}$$

Foundation species:

a single species that defines much of the structure of a community by creating locally stable conditions for other species; other terms, such as keystone species, ecosystem engineers, or dominant species, have similar meanings and overlap in their definitions

with the effects of each other level held constant. The values for the relative fitness of individuals, groups, and communities, in turn, were multiplied by the values for individual phenotype, average group phenotype, or average community phenotype to yield an expression that summarized total selection for any trait identifiable across individual, group, and community levels. This aspect of the multilevel approach is important because it offers an empirical answer to the widely held assumption that among-group or among-community variation will always be smaller in magnitude and similar in sign when compared with individual-level variation. The application of a contextual approach allows partitioning of each level's relative importance for total selection, which has been applied to laboratory analyses of communities (Goodnight 1990a,b; Goodnight & Craig 1996). Contextual analyses within species provides convincing evidence that family and group selection are responsible for significant evolutionary change (Goodnight et al. 1992, Stevens et al. 1995; see review in Wade 2016).

Although the multilevel selection approach identifies components of fitness that have arisen over evolutionary time (see also Queller 2014), it does not specifically measure the differential extinction or proliferation of communities. Selection imposed on host organisms supporting communities does produce this type of result and could be quantified in the same way, wherein a particular host phenotype (e.g., phenology) correlates with a community's ability to survive or reproduce (Smith et al. 2015). Thus, the covariance between host phenotype, Z_{host} , and its fitness relative to other hosts, w_{host} , $\text{Cov}[Z_{\text{host}}, w_{\text{host}}]$, could serve as a proxy for community-level selection. Alternatively, community phenotype can be represented using multivariate statistics (Shuster et al. 2006, Whitham et al. 2012). The covariance between a particular community phenotype, Z_C , and its fitness relative to other communities, w_C , $\text{Cov}[Z_C, w_C]$, could provide a similar and perhaps more accurate measure of community-level selection, particularly if communities are closely associated with particular host species individuals (see Section 5.2.1, below).

When community phenotype is difficult to quantify, but differential survival and proliferation can be measured, the opportunity for community selection provides an estimate of the maximum change in community phenotype resulting from an episode of selection. Here, the variance in the relative fitness of communities, measured in terms of the survival and proliferation of foundation species individuals, equals the variance in community fitness divided by its squared average, or $V_{W \text{ community}} / W^2_{\text{community}}$. If some measure of community fitness such as productivity is available, where C_{prod} and $V_{C_{\text{prod}}}$ equal the average and variance in community productivity, respectively, and where p_S and p_0 equal the proportions of surviving and extirpated communities, respectively ($p_S + p_0 = 1$), then, following Wade & Shuster (2004), the total variance in fitness would consist of two components, the average variance in community fitness within surviving communities, evaluated as $(p_S)(V_{C_{\text{prod}}})$, plus the variance in the average community fitness that exists between the surviving and the extirpated communities, evaluated as $C^2(p_0)(p_S)$.

The following sections provide empirical examples that use the above conceptual framework. In our evaluation of community evolution, we emphasize that a multilevel selection approach assumes the existence of evolutionary processes occurring at individual, group, and community levels. This approach does not assume the a priori predominance of any level. We consider these processes to be more common than is currently appreciated, and when taken together at all levels, they lead to the evolution of complex communities.

3. EVIDENCE OF PHENOTYPIC VARIATION AT THE COMMUNITY LEVEL

3.1. Effects of Genetic Variation on Community Phenotype

The generation of variation in community phenotype is crucial for the evolutionary process because it provides variation for selection to act on whole communities. Among plants, variation in

community phenotype is determined by intraspecific differences in many functional traits (e.g., phenology, growth, phytochemistry; see reviews in Whitham et al. 2012, Crutsinger 2016, Des Roches et al. 2018). When all of these traits are combined, the differences among plant genotypes can be so great that different genotypes have different community phenotypes supporting distinct communities of organisms and ecosystem processes. For example, Whitham et al. (2012) found that of 75 communities evaluated, 85% significantly differed in community composition among genotypes of the focal plant species (28 genera from 15 plant families that included trees, shrubs, forbs, and grasses). At a finer level, aboveground arthropod and plant communities responded most strongly, with 94% and 89% significantly affected by plant genotype, respectively, while belowground litter/soil invertebrates and microbial communities were significantly affected by plant genotype in 75% of the studies. Organisms exhibiting significant community associations to individual plant genotypes represented a wide range of interactions, including mutualism, parasitism, commensalism, facilitation, and competition.

The genetic population structure of organisms can also influence variation in community phenotype. Genetically dissimilar plants of the same species support more distinct communities than genetically similar plants (Bangert et al. 2006a,b; Zytynska et al. 2011, 2012). For example, in a common garden, Barbour et al. (2009b) found that the greater the differences in quantitative traits of phytochemistry and morphology were among eight races of *Eucalyptus globulus*, the greater the differences were in their associated communities.

3.2. Strong Interactors Influence Community Phenotype

Since interactions among species are responsible for generating the variation in community phenotype for selection to act upon, here we review the various types of IIGEs that are likely to be widespread and measurable in the field.

3.2.1. Foundation species. Which species are likely to have genetics-based interactions that impose IIGEs on other species and whole communities? Foundation species are prime candidates. Ellison et al. (2005) concluded that dominant species, keystone species, ecosystem engineers, and other strong interactors qualify as foundation species, which are defined as species that create locally stable conditions for other species by modulating and stabilizing fundamental ecosystem processes. Thus, IIGEs imposed by interacting foundation species, because of their strong influence on associated species, disproportionately affect the expression of community phenotypes.

3.2.2. Unidirectional interactions. If genetics-based interactions among species (i.e., IIGEs) (Shuster et al. 2006, Allan et al. 2012) affect evolution at higher levels, interaction networks are expected to reveal the underlying components of IIGEs. For example, in a common garden experiment with coastal willow *Salix hookeriana*, Barbour et al. (2016) found that plant resistance traits affected the abundances of four galling insect species, which in turn affected the abundances of six insect parasitoids, such that willow genotypes differed by 73% in the average composition of their trophic interactions. Simulations revealed that increasing plant genetic diversity from 1 to 26 different genotypes increased food web complexity by 20%, which further increased genetics-based community structure. In another common garden study, Lau et al. (2016) used community interaction network analysis to show that 44 species of arthropods were significantly affected by *Populus angustifolia* genotype (**Figure 2**). For example, susceptible tree genotypes attracted highly interactive herbivores or groups of species whose presence directly and indirectly

Interacting foundation species: genetics-based interactions of foundation species play an especially important role in defining communities and ecosystems; this term recognizes that not all interactions are equal—or, in other words, interactions that are based on genetic variation in foundation species are important because they affect hundreds of other species and can define ecosystems

Community interaction network (genotype-species network): genetic variation in foundation species that predictably influences the structure of the ecological network in complex communities

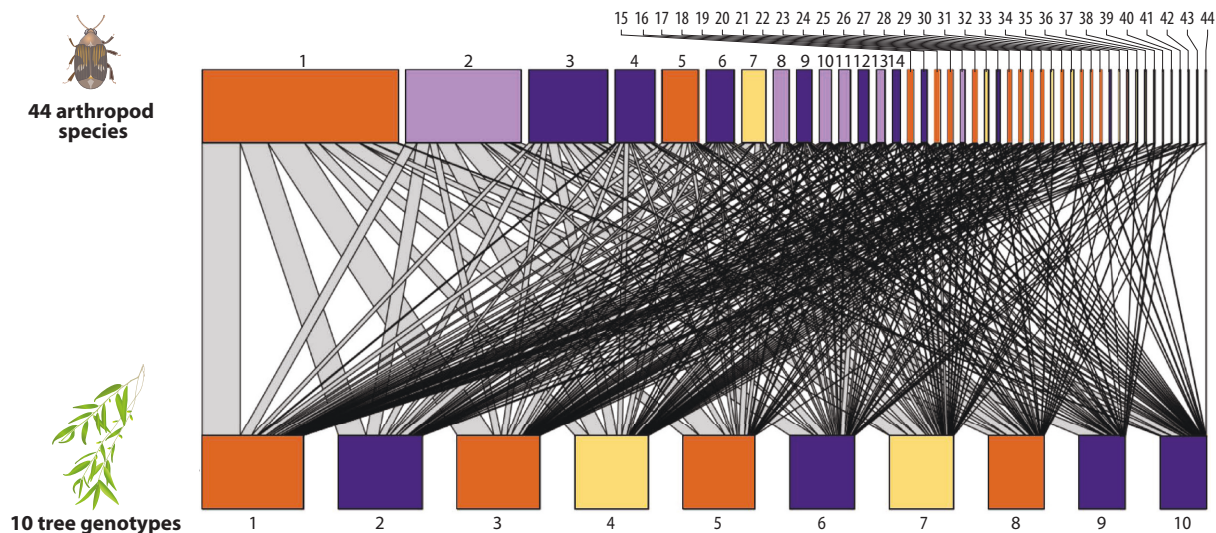


Figure 2

An arthropod community of 44 canopy species (*top nodes*) shows a nonrandom interaction network that differs among 10 different replicated genotypes of *Populus angustifolia* planted at random in a common garden (*bottom nodes*). Nodes are scaled by their totals of arthropod species richness and abundance. Nodes are arranged in order of increasing interactions, which corresponds to increasing centralization (i.e., a tendency for one or a few nodes to dominate the edges of the network) from right to left. Different colors represent different module membership (i.e., groups of interacting species). Lines represent interactions between individual tree genotypes and individual arthropod species scaled by the average abundance of each arthropod species across all individuals in a given genotype. Figure adapted from Lau et al. (2016).

attracted or repelled other species. Thus, genetics-based interactions contributed to the structure of direct and indirect interactions among trees and their associated arthropod community.

Not only do individual plant genotypes support different communities on the same plant, but also these communities may covary with one another such that one community (e.g., plant pathogens) may interact with another community (e.g., arthropods) to produce community genetic correlations (Lamit et al. 2015a). Thus, IIGEs can occur between two species or can involve multiple communities, resulting in repeatable patterns in community phenotype. Lamit et al. (2015a) estimated community genetic correlations from community abundances of twig endophytes, ectomycorrhizal fungi, soil bacteria, soil fungi, epiphytic lichens, foliage arthropods, and fungal leaf pathogens on replicated tree genotypes in a common garden (**Figure 3**). These tests showed moderate to strong community–genetic correlations, in which changes in the composition of one community among plant genotypes were mirrored by changes in the composition of other communities.

Because these community–genetic correlations may result from interactions between communities or both communities may be attracted to the same plant genotypes without interactions being involved, experiments are needed to separate these alternative hypotheses. For example, Busby et al. (2015) showed that with the addition of a common leaf pathogen, the arthropod community sharply declined relative to controls, confirming that they strongly interact (see Section 3.2.4). Thus, if selection were to favor particular tree genotypes resistant to a particular pathogen community, a whole suite of interacting communities may be affected, as depicted in **Figure 3**.

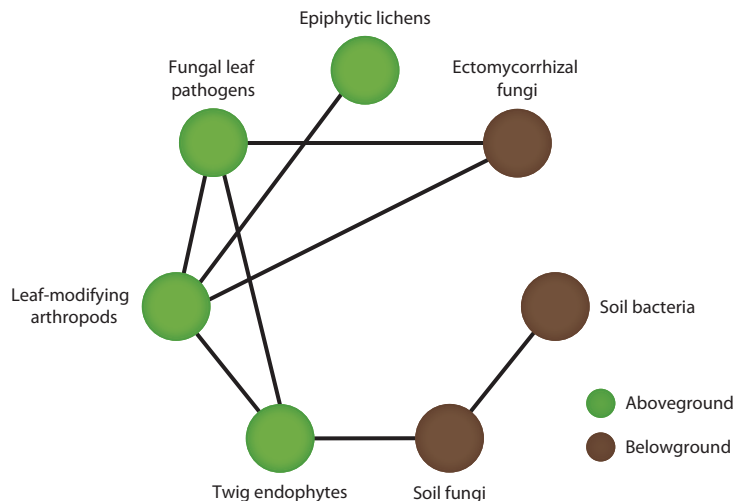


Figure 3

Common garden studies show that significant community genetic correlations exist among communities of twig endophytes, ectomycorrhizal fungi, soil bacteria, soil fungi, epiphytic lichens, leaf- or stem-modifying arthropods, and fungal leaf pathogens. Individual tree genotypes that supported a unique assemblage of species for one community were also likely to support a unique assemblage of species for a different community, and these communities covaried within tree genotypes. These tests showed moderate to strong community–genetic correlations, which were defined as changes in the composition of one community among plant genotypes that are mirrored by changes in the composition of another community. Almost half of all of the possible pairwise comparisons were significant, demonstrating a high level of genetics-based structure and interactions that define very different communities. Figure adapted with permission from Lamit et al. (2015a).

3.2.3. Reciprocal interactions. In addition to foundation species being strong interactors, some communities may be especially important because their combined effects provide important feedbacks that can enhance phenotypic variation, that is, reciprocal IIGEs. These include microbial communities that can positively or negatively affect plant performance (e.g., decomposers, mycorrhizae, and pathogen communities can feed back to affect plant performance). Although no single species may stand out, as a community they can affect plant performance with nutrient cycling and water uptake (see reviews in Fischer et al. 2014, Ware et al. 2019).

3.2.4. Experimental elimination or addition of interactions. The experimental breakup of IIGEs is expected to influence the among-community variance in phenotype as well as the fitness of community members lacking such interactions, as shown in laboratory studies with *Tribolium* beetles (e.g., Goodnight 1990a,b; Goodnight & Craig 1996). In the field, Turkington & Harper (1979) argued that interactions between white clover (*Trifolium repens*) and each of four competing grass species resulted in effects consistent with IIGEs. When clover was grown next to its natal grass species, it outperformed nonnatal plantings in three out of four trials. In a similar experiment with *Populus fremontii*, *Salix exigua*, and *Salix gooddingii*, Grady et al. (2017) found that annual net primary productivity was greater for each of the three species when grown in sympatric blocks (all three species collected from the same site, where they may have adapted to one another) than in allopatric blocks (same genotypes used in sympatric blocks, but mixed from different collection sites). These experiments argue that individual species within a community have evolved different IIGEs when associated with different competitors.

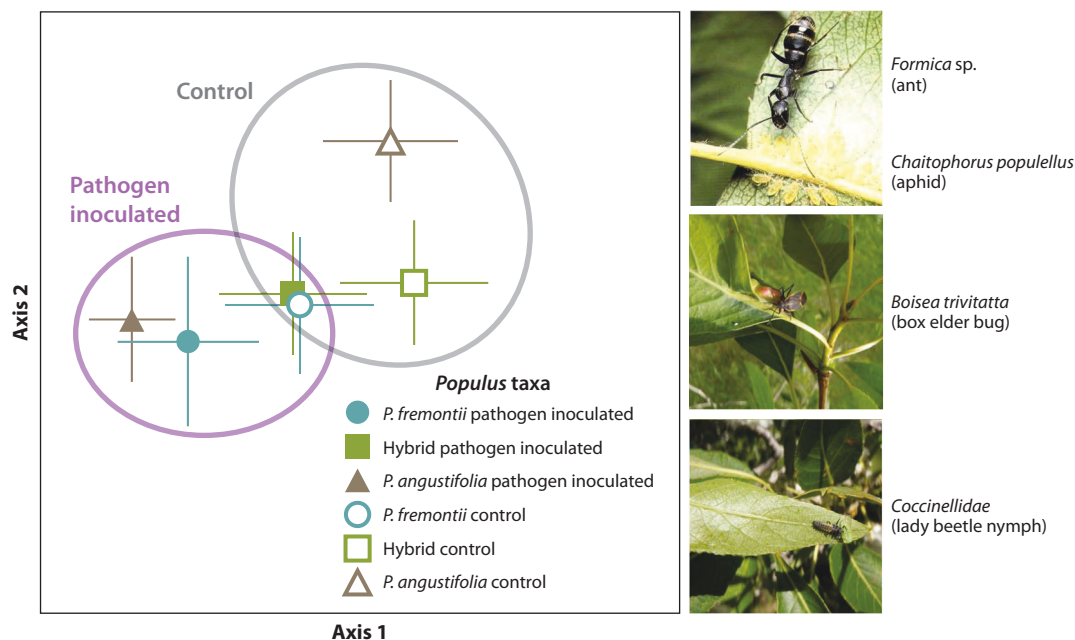


Figure 4

Nonmetric multidimensional scaling (NMDS) ordination shows that interspecific indirect genetic effects between foundation species create greater variation in community phenotypes for selection to act upon. In a common garden with different genotypes of *Populus fremontii*, *Populus angustifolia*, and their natural hybrids, the genetics-based plant–pathogen interaction predictably affected a foliar arthropod community of 32 species, including herbivores, predators, scavengers, and parasites, to produce new community phenotypes. In this ordination analysis, each symbol represents the arthropod community supported by the genotypes of each tree species and their hybrids. On control trees without pathogens, the arthropod communities of each tree cross type significantly differed from one another. When an experimental group using the same genotypes was inoculated with pathogens, the plant–pathogen interaction produced a new set of community phenotypes that differed from one another and their corresponding cross types in the control group. Centroids ± 1 SE are shown for each treatment and control group. Thus, the interaction of two foundation species (the tree and a pathogen) effectively doubled the variation in arthropod community phenotypes that selection could act upon. Photos at right show typical species associated with tree cross types and treatment versus control groups. Abbreviation: SE, standard error. Figure adapted from Busby et al. (2015).

As a test of the importance of IIGEs generating variation in community phenotypes, Keith et al. (2017) experimentally removed the aphid *Pemphigus betae*, which forms galls on the cottonwood *Populus angustifolia* and affects an arthropod community of 139 species. Because the interaction networks on aphid-resistant and -susceptible trees differed greatly, the presence of aphids generated more community phenotypes than when aphids were absent, as is expected when genetic and associated environmental interactions exist. Busby et al. (2015) showed a similar effect of a genetics-based plant–pathogen interaction in generating increased variation among arthropod community phenotypes, which effectively doubles the observed arthropod community phenotypes that can arise via IIGEs (Figure 4). Studies of the fungal leaf pathogen *Drepanopeziza populi* on *Populus* spp. have shown genetic variation in symptom severity (e.g., leaf necrosis, premature leaf abscission; Busby et al. 2013) that can result in reduced growth, canopy dieback, and mortality (Ostry & McNabb 1985). In a common garden experiment, Busby et al. (2015) found that plants inoculated with the leaf pathogen and control plants without the pathogen supported very different arthropod community phenotypes. Because pathogens negatively affect their host plants and there is significant variation in pathogen resistance within and among cross types of *P. fremontii*,

P. angustifolia, and their natural hybrids, selection acting on the tree is also acting on a diverse arthropod community of herbivores, predators, scavengers, and parasites.

3.3. Environmental Influences on Interspecific Indirect Genetic Effects

Gene-by-gene-by-environment interactions are known to affect the evolutionary process (e.g., Wade 2016). Here we review some of these interactions to show how they can change across the landscape, how they can affect entire communities, and how common garden studies can facilitate their quantification.

3.3.1. Environmental gradients. Changes in latitude or elevation produce environmental gradients that alter plant phenotype (Smith et al. 2011, Cooper et al. 2019). Such changes are expected to shift the nature of IIGEs on particular host genotypes, which in turn may cause their associated communities and interactions to change (Gilman et al. 2010). Evans et al. (2016) used common gardens of the same tree genotypes of *P. angustifolia* reciprocally planted across their natural range from Arizona, USA, to Alberta, Canada, to investigate evidence of past selection on bud phenology and tree growth. They found that, compared with an observed lack of genetic structure for neutral genetic sequence data, there was evidence of strong phenotypic differentiation in these functional traits associated with their latitude of origin, emphasizing the role climate has played in divergent selection throughout this species' range. Consistent with this result, the arthropod community of 53 species measured on tree populations within a common garden were distinct from one another in a way consistent with tree trait divergence, and community metrics were positively correlated with tree productivity. These results suggest that divergence in key tree traits affects differentiation in associated arthropod communities. Similarly, in a common garden experiment in which eight geographical races of *E. globulus* were planted together, significant environmentally induced differences in tree phytochemistry and leaf morphology led to differences in associated arthropod and fungal communities (Barbour et al. 2009b).

3.3.2. Phenotypic plasticity at the community level. The ability of an organism to express different phenotypes in response to different environmental conditions (West-Eberhard 1989) can affect community richness, abundance, resiliency, and IIGEs. The phenotypic plasticity at the community level of a foundation willow species affected both above- and belowground species richness to a greater degree than its intraspecific genetic variation (Barbour et al. 2019). When the environment changes, phenotypic plasticity in traits related to resource use can alter a species' fundamental and realized niche, affecting the niche space of other species and the degree of species coexistence and diversity within the community (Berg & Ellers 2010). For example, with an arthropod community of more than 250 species on pinyon pine (*P. edulis*), Stone et al. (2018) found that during a drought, species richness and abundance were greatly depressed but that the following year, when conditions improved, the community rebounded (**Figure 5**). However, the degree of community resiliency (i.e., the ability to return to predisturbance composition) was greatly affected by the tree's resistance to the scale insect *Matsucoccus acalyptus*. Arthropod diversity and abundance on pinyons that were genetically susceptible to scale insects exhibited no community response (i.e., shallow reaction norm), whereas pinyons resistant to scale insects showed large community responses over time (i.e., steep reaction norm). Additionally, when scales were removed from genetically susceptible trees and allowed to recover, these otherwise scale-susceptible trees had the same reaction norms as genetically resistant trees, demonstrating that scales were a causal agent of community change. Thus, the plasticity in IIGEs of individual plant genotypes and an insect herbivore in response to drought define arthropod community phenotype and enhance variation in community phenotypes.

Phenotypic plasticity at the community level

level: a change in an organism's traits with a change in environment that results in a change in community phenotype

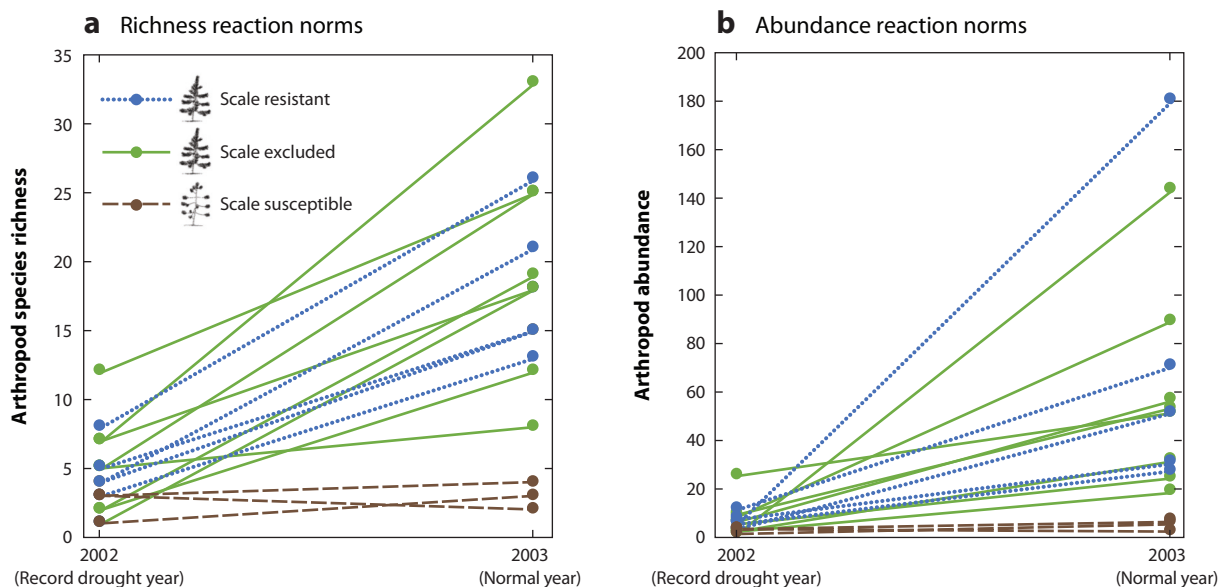


Figure 5

In a community of more than 250 arthropod species, reaction norms show that the phenotypic plasticity of *Pinus edulis* genotypes is genetically variable and defined by environmental change (drought) and interspecific indirect genetic effects with the scale insect *Matsucoccus acalyptus*. The year 2002 was a record drought year, while 2003 was near normal. Tree outlines show that resistant trees support a full complement of needles, whereas the feeding of many thousands of scales causes premature needle abscission, giving susceptible trees their distinctive “poodle tail” architecture. Each line represents the reaction norm for an individual tree genotype ($n = 16$ tree genotypes). (a) The change in arthropod species richness for individual tree genotypes in the drought year 2002 followed by the normal year 2003. Scale-susceptible tree genotypes exhibit little or no community response (brown dashed lines), while scale-resistant genotypes exhibit high community response (blue dotted lines). Scale-susceptible trees with scales experimentally excluded for 15 years or more are indistinguishable from scale-resistant trees (green solid lines), confirming that tree genotype interactions with scales cause a change in tree community phenotype and that climate interacts with tree genotype to affect plasticity at the community level. (b) The same general pattern in reaction norms is observed with arthropod abundance for the same individual tree genotypes shown in panel a. Figure adapted from Stone et al. (2018).

4. EVIDENCE OF COMMUNITY HERITABILITY

4.1. Estimates of Community Heritability

Community heritability is essential to quantify because not all genetic variation is heritable and responsive to selection. Estimates of community heritability are based on individual plant genotypes that have been clonally replicated and randomly planted in a common garden. Such studies have estimated H^2_C for arthropods (Shuster et al. 2006, Keith et al. 2010), soil-decomposing fungi and bacteria (Schweitzer et al. 2008), twig endophytes (Lamit et al. 2014), ectomycorrhizal mutualists (Lamit et al. 2016), lichens (Lamit et al. 2015b), pathogens (Busby et al. 2013), and aquatic macroinvertebrates (Compson et al. 2016). Ecosystem traits of individual plant genotypes including decomposition, nitrogen mineralization, trophic structure, biodiversity, and community stability (Bailey et al. 2006; Schweitzer et al. 2008, 2012; Keith et al. 2010, 2017) can also be heritable. In combination, these heritable traits are reflected by IIGEs that produce genotype-specific community interaction networks (Lau et al. 2016) and community–genetic correlations (Lamit et al. 2015a). Because different genotypes support different communities, significant community heritability underscores why plant genetic diversity is crucial to maintain biodiversity (e.g., Wimp et al. 2004; Bangert et al. 2006a,b; Hughes et al. 2008; Ferrier et al. 2012).

Community stability:

the similarity in the community composition of associated species across years for individual foundation species' genotypes or populations

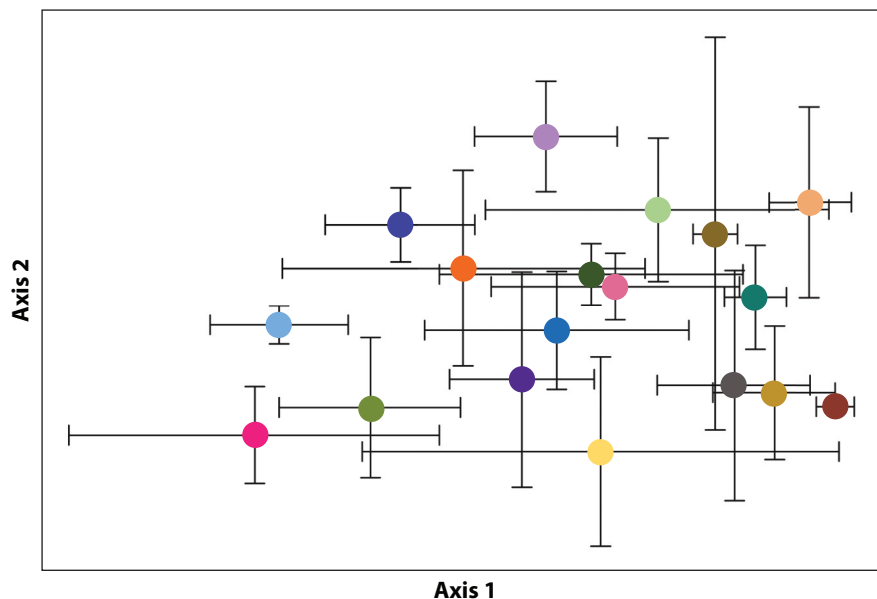


Figure 6

The lichen community comprising nine species found on *Populus angustifolia* is a heritable plant trait that is largely defined by bark roughness, which varies among tree genotypes. Nonmetric multidimensional scaling (NMDS) ordination was used to graphically present tree genotype/community findings. Each colored symbol represents the lichen community composition of an individual tree genotype ± 1 SE and its replicate clones planted at random in a common garden (18 tree genotypes with two to nine replicates per genotype; 76 total trees). The effect of tree genotype on species richness was tested with REML-based linear models. Variance components were used to estimate broad-sense community heritability ($H^2_C = 0.20$). The differences among lichen communities were most closely associated with differences in bark roughness traits among tree genotypes of the same age, which was also a heritable trait ($H^2 = 0.48$). In general, rougher-barked tree genotypes supported greater lichen cover that differed in lichen composition from that of smoother-barked tree genotypes. Structural equation modeling further supported the hypothesis that genetic variation in rough bark is a mechanism linking tree genes to variation in lichen communities. Abbreviations: REML, restricted maximum likelihood; SE, standard error. Figure adapted from Lamit et al. (2015b).

One of numerous community heritability examples is the lichen community on trees, even though these epiphytes that use another organism as a substrate might seem insensitive to individual tree genotypes. Lamit et al. (2015b) quantified how a lichen community of nine species was distributed among genotypes of *P. angustifolia* in a common garden (**Figure 6**). They found significant broad-sense heritability in which different tree genotypes supported different lichen communities ($H^2_C = 0.20$). The differences in lichen communities were most closely associated with differences in bark roughness traits, which were also heritable ($H^2 = 0.48$). Similar findings have been observed with a community of 180 arthropod species associated with heritable variation in bark traits of *E. globulus* in Australia (Barbour et al. 2009a).

Hidden players such as soil microbial communities can differentially interact with individual plant genotypes to fundamentally affect ecosystem processes such as decomposition and nutrient cycling. Schweitzer et al. (2008) quantified the soil microbial community on replicated genotypes of *P. angustifolia* and found a broad-sense community heritability of $H^2_C = 0.78$, which is important because the soil microbial community affects biomass carbon and nitrogen pools. These microbial differences in community composition were most closely related to intraspecific genetic variation

in leaf condensed tannins that slow down decomposition. Schweitzer et al. (2012) subsequently quantified significant broad-sense heritability of the annual rates of net nitrogen mineralization ($H^2 = 0.66$) that can feed back to affect other plant traits such as fine root production (Fischer et al. 2014).

4.2. Evidence of Community Heritability over Time

If community heritability is consistent over time, the potential for directional selection to act on community phenotypes is enhanced relative to communities that are more variable in their heritability. Keith et al. (2010) quantified the composition of 103 arthropod species for three consecutive years for the same genotypes of *P. angustifolia* in a common garden. They found that community heritability in each of the three years was $H^2_C = 0.60, 0.66$, and 0.62 , demonstrating that community heritability was highly repeatable. The consistency of community composition across years also provides a quantitative measure of community stability that significantly differs among tree genotypes. Depending on tree genotype, community similarity across years ranged from 24% to 61%, and community stability was shown to be a significantly heritable trait ($H^2_C = 0.32$). These findings show that community heritability can be consistent over time and that community stability is genotype dependent. With many examples of significant community variation that is heritable, we next examine whether selection acts upon this variation.

5. EVIDENCE OF COMMUNITY SELECTION RESULTING IN EVOLUTION

5.1. Laboratory Examples

Community evolution is the outcome of selection operating at multiple levels that results in the differential survival and proliferation of communities. Although we emphasize complex natural communities, laboratory studies of community-level selection paved the way for addressing community evolution in the wild. Goodnight (1990a,b) and Goodnight & Craig (1996) observed that community-level selection imposed on high and low productivity in two-species communities of *Tribolium* beetles led to positive responses in each species, as well as to correlated responses in productivity and emigration rate occurring within and between species. This result confirmed that community-level selection on heritable community-level traits leads to evolutionary change in the average community phenotype. In another system, Swenson et al. (2000a,b) imposed community-level selection on soil and pond microbial communities on the basis of both the dry weight of plant biomass the community could support and its ability to decompose 3-chloroaniline, as well as on the pH generated by pond microbial communities within their aquatic habitats. The authors favored communities that generated high and low extremes in a community phenotype that arose through the combined interactions of community members. They identified community heritability as significant among-community variance in traits associated with interspecific competitive outcome within communities, providing a genetic explanation for why community-level selection led to a change in the average community phenotype.

5.2. Field Examples

Demonstrating evidence of selection and evolution at the community level is critical for understanding complex communities in the field. We present two examples based on studies in the wild followed by common garden studies that document genetics-based evidence for community phenotypic change over time or space.

5.2.1. Goldenrod. *Solidago velutina* and other native plants, including aspen, are heavily browsed by introduced Rocky Mountain elk (*Cervus canadensis nelsoni*) in Arizona, USA. After elk fences were constructed to protect vegetation, Smith et al. (2015) found that goldenrod growing inside the fences flowered 3 weeks earlier than plants immediately outside, where they also supported a different pollinator/arthropod community. These findings suggest that elk imposed selection on *S. velutina* outside the fences, causing these plants to diverge in phenotype relative to those inside, and, concomitantly, that IIGEs influencing the communities these plants supported had also changed.

To test the hypotheses that phenological and community differences were genetically based and that selection on host plants can lead to a change community phenotype, Smith et al. (2015) collected seeds from goldenrod growing inside and outside the fences, germinated them in the greenhouse, and planted them back into the wild in an enclosed common garden. In the second growing season, the flowering phenologies and arthropod communities of progeny plants resembled those of their parents, confirming that introduced elk imposed selection that changed flowering phenology as well as the pollinator/arthropod community. Overall, this study quantified genetic variation underlying goldenrod and its community phenotype inside and outside the elk fence, as well as the heritability of flowering phenology and the pollinator/arthropod community. Moreover, it demonstrated that selection on the host plant changed the frequency of IIGEs capable of influencing community phenotype and thus changed the frequency of particular phenotypes among communities. If the frequency of particular IIGEs among communities changes, the average community phenotype will also change. Thus, selection on host genotype led to an evolutionary change in the arthropod community phenotype in which different arthropod community phenotypes were supported by changes in plant phenology.

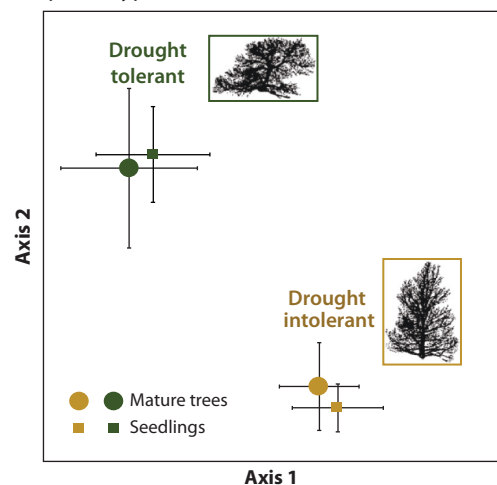
5.2.2. Pine. A 32-year study of pinyon pine (*P. edulis*) showed an adaptive, genetics-based change in its ectomycorrhizal fungal (EMF) community phenotype accompanying a change in climate (Williams et al. 2020) that greatly affected the survival and distribution of dominant plant species throughout the American Southwest (Mueller et al. 2005, Brusca et al. 2013). Two groups of trees that differed in architecture and insect herbivory were found to be genetically distinct in their ability to withstand drought (Sthultz et al. 2009a). Long-term EMF studies showed that trees with a shrub-like architecture were drought tolerant and were dominated by fungal species in the phylum Ascomycota. In contrast, trees with upright architecture were drought intolerant and were dominated by fungal species in the phylum Basidiomycota (Sthultz et al. 2009b). Community phenotype was heritable because seedlings from the two tree groups inoculated with EMF communities acquired them only from their parental groups (**Figure 7a**) (Gehring et al. 2017). The reciprocal experiment, in which trees received the EMF inoculum of the opposite tree type, could not be performed because of the high specificity of EMF communities to either tolerant or intolerant seedlings.

These consistent differences in EMF communities between the two groups of pinyons contributed strongly to their differences in drought tolerance. When drought-tolerant seedlings were inoculated with their tolerant EMF community, they achieved nearly twice the growth rate of intolerant seedlings when inoculated with their EMF community, and both performed better than control plants that grew in sterile soil without EMF communities in drought conditions (**Figure 7b**) (Gehring et al. 2017, Patterson et al. 2019). Thus, EMF communities benefit both tree types and are specific to their tree types, but the EMF communities of tolerant trees provided greater positive feedbacks than those of intolerant trees in dry conditions and generated distinct community phenotypes with respect to drought tolerance. Furthermore, in the absence of their specific EMF communities, intolerant and tolerant seedlings did not differ in growth,

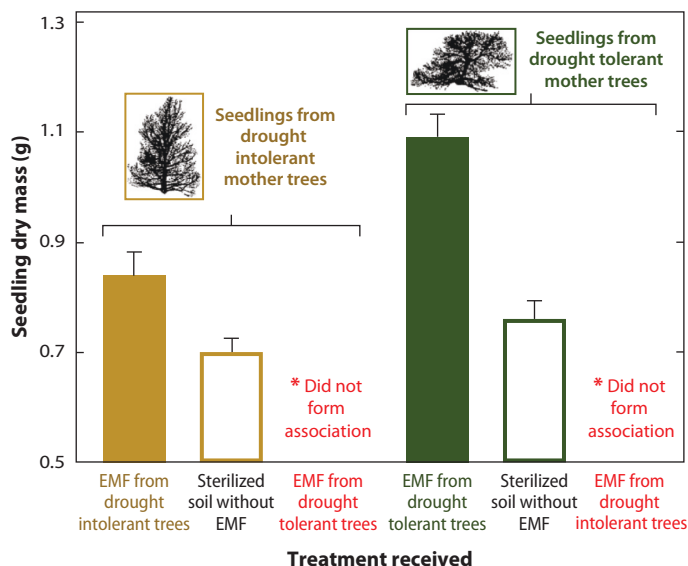
but when inoculated with their distinct EMF communities, tolerant seedlings outperformed intolerant seedlings; in other words, EMF community differences drive the different responses to environmental change.

Record drought in 2002 changed the genetic structure of the tree population such that drought-intolerant trees suffered 68% mortality compared with only 21% mortality for drought-tolerant trees (**Figure 7c**) (Stultz et al. 2009a). The EMF community phenotype also changed after the drought. Tolerant trees changed little in their EMF communities before and after the drought; however, the population of intolerant trees dramatically changed its EMF communities via tree mortality and EMF community death. Surviving intolerant trees also exhibited a shift in their

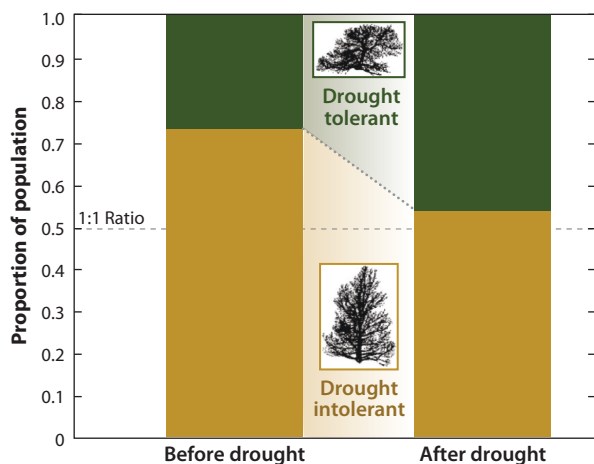
a Variation and heritability of community phenotype



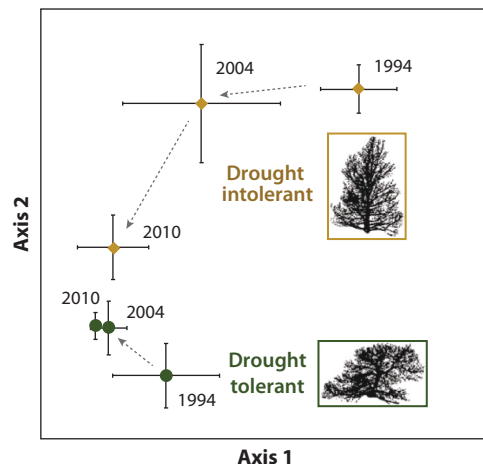
b Feedbacks of EMF community on foundation tree



c Selection resulting in evolution of foundation tree



d EMF community selection resulting in evolution



(Caption appears on following page)

Figure 7 (Figure appears on preceding page)

Community evolution involving selection acting on drought-tolerant and -intolerant genotypes of *Pinus edulis* and its ectomycorrhizal fungal (EMF) community in response to climate change. Tree icons represent the different architectures of these tree classes in which drought-tolerant genotypes have a shrub-like architecture and drought-intolerant genotypes have an upright architecture (for more explanation of architecture differences, see Sthultz et al. 2009a). (a) A nonmetric multidimensional scaling (NMDS) ordination of the EMF communities on drought-tolerant and -intolerant mature trees (*large dots*) and seedlings (*small squares*). EMF communities differ for each tree drought-tolerance class (variation in community phenotype), and seedlings acquire the same EMF communities as mature trees in their respective drought-tolerance class, demonstrating that the community is heritable. (b) Drought-tolerant seedlings benefit nearly twice as much from receiving drought-tolerant EMF communities as drought-intolerant seedlings benefit from receiving drought-intolerant EMF communities (*solid bars*). The reciprocal experiment, in which each receives an EMF community from the other tree class, could not be conducted because seedlings did not form associations with EMF communities from the other tree class (represented by *red asterisks*). This reflects a high level of specificity in which seedlings acquire only the EMF communities of their respective tree class. When seedlings were grown in sterile soil without EMF communities (*open bars*), seedling performance declined relative to those with EMF communities, demonstrating that both tree classes benefit from the positive feedbacks from their EMF communities, but tolerant seedlings benefit much more than intolerant seedlings. (c) Before a record drought, drought-intolerant trees dominated the population, but after the drought, they were nearly equally abundant, demonstrating that selection differentially acted on the tree population, resulting in a change in the tolerant/intolerant phenotypes (an example of selection acting at the individual level). (d) Nonmetric multidimensional scaling (NMDS) ordination shows that selection acts on the EMF community. The EMF communities on drought-tolerant trees changed little from 1994 to 2010, whereas the EMF communities on drought-intolerant trees changed greatly over the same time span (an example of selection differentially acting on EMF communities over time). Panels *a* and *b* adapted from Gehring et al. (2017). Panel *c* adapted with permission from Sthultz et al. (2009a). Panel *d* adapted with permission from Gehring et al. (2014).

EMF communities to more closely resemble those of tolerant trees, but the two groups remained significantly different in composition (**Figure 7d**) (Gehring et al. 2014).

In summary, for these pinyon/EMF communities, genetics-based variation in community phenotype was demonstrated and the community phenotype was shown to be heritable. Community-level selection due to drought favored drought-tolerant trees with their associated EMF communities that provided better protection from drought than drought-intolerant EMF communities, and the proportion of drought-tolerant communities increased. In effect, these tree types and their associated communities experienced selection as functional units with high relative fitness; that is, they were adaptive (Wilson 1975, 2016).

5.2.3. The opportunity for community-level selection. Using the pine example and the method described in Section 2.3.3, we estimated the opportunity for community-level selection. We combined the average and variance in productivity for the surviving communities with the proportions of surviving and extirpated communities (**Figure 7**) to estimate the mean and variance in relative community fitness (cf. Wade & Shuster 2004). We first estimated the variance in fitness within and between both sets of tree/EMF communities. We then estimated the opportunity for selection before ($I = 0.09$; $N_{\text{trees}} > 1,000$) and after the drought ($I = 3.3$; $N_{\text{trees}} = 892$). Lastly, we partitioned the opportunity for community-level selection into pre-drought and post-drought components. We found that the total opportunity for community-level selection ($I = 0.64$) was more than seven times stronger than the opportunity for community-level selection during pre-drought conditions. This partitioning also showed that more than 71% of the total opportunity for community-level selection occurred between the pre- and post-drought intervals, a selection event that changed the relative proportions of drought-tolerant and drought-intolerant trees and their communities.

To help readers appreciate the magnitude of the opportunity of community-level selection in the pinyon system, we compare our findings with a major human disease outbreak, the bubonic plague pandemic of the mid-fourteenth century (the Black Death). One-third of the European population died, and the opportunity for selection during this event was $I = 0.84$. In contrast,

during the American Southwest megadrought from 2000 to 2018 (Williams et al. 2020), the opportunity for selection, $I = 3.3$, on *P. edulis* communities was nearly four times stronger (Herlihy 1974; S.M. Shuster, unpublished data). In other words, community-level selection can be intense, and with ongoing climate change, this higher level of selection may be critical for assessing its impacts on whole communities.

The EMF species compositions were strongly determined by pinyon tree genotype (Gehring et al. 2017), suggesting that the variance in fitness of individuals and groups within these fungal communities was strongly determined by the overall fitness of the communities in which they were found (i.e., drought-tolerant versus drought-intolerant communities). Thus, if the opportunity for community-level selection represents the maximum possible strength of selection due to that episode of selection, then all lower levels of selection, and particularly the selection coefficients on individual traits within these lower levels, were likely nested within this community-level selection opportunity (Hersch & Phillips 2004). It seems likely that the catastrophic mortality of foundation species due to droughts, fires, storms, and other increasingly common global change events is imposing previously unimagined evolutionary consequences on biodiversity.

6. CONCLUSIONS

We present two lines of evidence challenging the dogma that selection is largely, if not exclusively, restricted to the individual level (Williams 1966). First, in studies of complex communities in nature, we show that significant variation in community phenotypes exists, that these phenotypes are heritable, and that selection can occur at the community level, resulting in community evolution. Second, our findings argue that selection can and likely does act at multiple levels from individuals to communities.

Experimental findings of community heritability, community interaction networks, community genetic correlations, and interaction removal studies show genetics-based community structure (i.e., different genotypes support different communities and interactions) that cannot be explained by neutral theory, or the equivalency of species as interchangeable units (Hubbell 2001, 2005). These findings refute the notion that local communities have little to contribute to our understanding of ecology and evolution (Ricklefs 2008). They also argue that evolutionary biologists need to focus far more on species interactions, as they are essential to accept or refute higher levels of selection and to understand the relative roles of individual-, group-, and community-level selection on organizing complex ecosystems. The finding by Compson et al. (2016) that the genotypes of leaf litter produced in a riparian terrestrial ecosystem affect community composition and emergence of macroinvertebrates in an adjacent aquatic ecosystem demonstrates that the community genetic footprint of plant genotypes can extend beyond the local environment of an individual plant. Just how far these genetic effects extend is unknown, but several studies have shown that plant genetic diversity can extend to the stand level in nutrient cycling (e.g., Schweitzer et al. 2012) and to the stand and regional levels with species diversity (Wimp et al. 2004, Bangert et al. 2008). This genetics-based connectedness has the potential to greatly affect land manager policy, in which the choice of specific genotypes used in restoration can affect their survival in a changing environment as well as the diversity and stability of associated communities (e.g., Keith et al. 2010).

Most studies are not designed to go beyond quantifying selection acting solely at the individual level. The explicit inclusion of phenotypic variation, heritability, and selection at each level of biological organization allows consideration of the relative importance of each of these factors for the overall evolutionary process. The use of multivariate statistics to visualize community phenotypes and to quantify community heritability allows community genetics to be explored

with well-established quantitative genetics methodology. An important research frontier will involve testing for community evolution in complex systems by quantifying genetic variation and structure among community members, as well as accounting for interspecific trait interactions that produce IIGEs. The need to quantify the genetic basis of interactions is emphasized, for example, by the ecosystem consequences of beavers in Yellowstone National Park. Using repeat photographs, Chadde & Kay (1991) found that with beavers and the ponds they created, there was a rich aquatic/riparian ecosystem, but once beavers and their interactions were lost, the dams, ponds, aspens, and willows disappeared to become a vastly different ecosystem of dry grassland. Although additional examples exist (e.g., otter–sea urchin–kelp interactions; Estes et al. 2016), we generally lack the underlying studies of the genetic basis of these interactions, so little can be said about their evolution and the communities they affect.

The genetic basis of community organization can be explored using common garden experiments with clonal, full-sib, or half-sib replication to quantify community heritability as well as associated differential performance and survival of these communities over time. Changes in biotic and abiotic environmental conditions, such as those resulting from IIGEs (**Figures 4 and 5**), climate change (**Figures 1, 5, and 7**), and introduced species (Smith et al. 2015), are common. They result in vegetation shifts, die-offs at the landscape level, changes in community composition, and community interaction networks and community genetic correlations (**Figures 2 and 3**) that provide ideal opportunities to evaluate community evolution in real time (**Figure 7**).

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The National Science Foundation IRCEB (Integrated Research Challenges in Environmental Biology), LTREB (Long Term Research in Environmental Biology), FIBR (Frontiers in Integrative Biological Research), MRI (Major Research Instrumentation), BEE (Bridging Ecology and Evolution), and Macrosystems Biology programs and BOR (Bureau of Reclamation) provided financial support. SEGA (Southwest Experimental Garden Array) with BOR, the Bureau of Land Management, The Nature Conservancy, the National Park Service, the US Forest Service, the Arizona Game and Fish Department, the Grand Canyon Trust, The Arboretum at Flagstaff, Babbitt Ranches, and the Ogden Nature Center provided long-term support to establish reciprocal common gardens/restoration sites essential for key research presented here. We thank Catherine A. Gehring for her generous efforts to develop the pinyon/ectomycorrhizal fungal community example and for commenting on drafts of the outline and manuscript. We thank Michael J. Wade, David S. Wilson, Douglas Futuyma, and two anonymous reviewers for their comments that improved the manuscript and Kara Skye Gibson for her illustrations.

LITERATURE CITED

- Allan GJ, Shuster SM, Woolbright S, Walker F, Meneses N, et al. 2012. Interspecific indirect genetic effects (IIGEs): linking genetics and genomics to community ecology and ecosystem processes. In *Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives*, ed. T Ohgushi, O Schmitz, RD Holt, pp. 295–323. Cambridge, UK: Cambridge Univ. Press
- Antonovics J. 1992. Toward community genetics. In *Plant Resistance to Herbivores and Pathogens*, ed. RS Fritz, EL Simms, pp. 426–49. Chicago: Univ. Chicago Press

- Bailey JK, Wooley SC, Lindroth RL, Whitham TG. 2006. Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecol. Lett.* 9:78–85
- Bangert RK, Allan GJ, Turek RJ, Wimp GM, Meneses N, et al. 2006a. From genes to geography: a genetic similarity rule for arthropod community structure at multiple geographic scales. *Mol. Ecol.* 15:4215–28
- Bangert RK, Turek RJ, Rehill B, Allan GJ, Wimp GM, et al. 2006b. A genetic similarity rule determines arthropod community structure. *Mol. Ecol.* 15:1379–92
- Bangert RK, Lonsdorf EV, Wimp GM, Shuster SM, Fischer DG, et al. 2008. Genetic structure of a foundation species: scaling community phenotypes from the individual to the region. *Heredity* 100:121–31
- Barbour MA, Erlandson S, Peay K, Locke B, Jules ES, Crutsinger GM. 2019. Trait plasticity is more important than genetic variation in determining species richness of associated communities. *J. Ecol.* 107:350–60
- Barbour MA, Fortuna MA, Bascompte J, Nicholson JR, Julkunen-Tiitto R, et al. 2016. Genetic specificity of a plant–insect food web: implications for linking genetic variation to network complexity. *PNAS* 113:2128–33
- Barbour RC, Forster LG, Baker SC, Steane DA, Potts BM. 2009a. Biodiversity consequences of genetic variation in bark characteristics within a foundation tree species. *Conserv. Biol.* 23:1146–55
- Barbour RC, O'Reilly-Wapstra JM, De Little DW, Jordan GJ, Steane DA, et al. 2009b. A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology* 90:1762–72
- Becker WA. 1985. *Manual of Quantitative Genetics*. Pullman, WA: Academic. 4th ed.
- Berg MP, Ellers J. 2010. Trait plasticity in species interactions: a driving force of community dynamics. *Evol. Ecol.* 24:617–29
- Bordenstein SR, Theis KR. 2015. Host biology in light of the microbiome: ten principles of holobionts and hologenomes. *PLOS Biol.* 13:e1002226
- Brusca RC, Wiens JF, Meyer WM, Eble J, Franklin K, Overpeck JT, Moore W. 2013. Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona mountain plant transect revisited. *Ecol. Evol.* 3:3307–19
- Busby PE, Lamit LJ, Keith AR, Newcombe G, Gehring CA, et al. 2015. Genetics-based interactions among plants, pathogens and herbivores define arthropod community structure. *Ecology* 96:1974–84
- Busby PE, Newcombe G, Dirzo R, Whitham TG. 2013. Genetic basis of pathogen community structure for foundation species in a common garden and in the wild. *J. Ecol.* 101:867–77
- Chadde SW, Kay CE. 1991. Tall willow communities on Yellowstone's northern range: a test of the "natural regulation" paradigm. In *The Greater Yellowstone Ecosystem*, ed. RB Keiter, MS Boyce, pp. 231–62. New Haven, CT: Yale Univ. Press
- Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18:117–43
- Compson ZG, Hungate BA, Whitham TG, Meneses N, Busby PE, et al. 2016. Plant genotype influences aquatic–terrestrial ecosystem linkages through timing and composition of insect emergence. *Ecosphere* 7:e01331
- Cooper HF, Grady KC, Cowan JA, Best RJ, Allan GJ, Whitham TG. 2019. Genotypic variation in phenological plasticity: Reciprocal common gardens reveal adaptive responses to warmer springs but not to fall frost. *Glob. Change Biol.* 25:187–200
- Crow JF. 1958. Some possibilities for measuring selection intensities in man. *Hum. Biol.* 30:1–13
- Crutsinger GM. 2016. A community genetics perspective: opportunities for the coming decade. *New Phytol.* 210:65–70
- Darwin C. 1859. *On the Origin of Species by Means of Natural Selection*. London: Murray
- Des Roches S, Post DM, Turley NE, Bailey JK, Hendry AP, et al. 2018. The ecological importance of intraspecific variation. *Nat. Ecol. Evol.* 2:57–64
- Douglas AE, Werren JH. 2016. Holes in the hologenome: why host–microbe symbioses are not holobionts. *mBio* 7:e02099-15
- Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586–608
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3:479–86

- Estes JA, Burdin A, Doak DF. 2016. Sea otters, kelp forests, and the extinction of Steller's sea cow. *PNAS* 113:880–85
- Evans LM, Allan GJ, Shuster SM, Woolbright SA, Whitham TG. 2008. Tree hybridization and genotypic variation drive cryptic speciation of a specialist mite herbivore. *Evolution* 62:3027–40
- Evans LM, Kaluthota S, Pearce DW, Allan GJ, Floate K, et al. 2016. Bud phenology and growth are subject to divergent selection across a latitudinal gradient in *Populus angustifolia* and impact adaptation across the distributional range and associated arthropods. *Ecol. Evol.* 6:4565–81
- Faith DP, Minchin PR, Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57–68
- Falconer DS, McKay TFC. 1996. *Introduction to Quantitative Genetics*. New York/London: Longman. 4th ed.
- Ferrier SM, Bangert RK, Hersch-Green E, Bailey JK, Allan GJ, Whitham TG. 2012. Unique arthropod communities on different host–plant genotypes results in greater arthropod diversity. *Arthropod Plant Interact.* 6:187–95
- Fischer DG, Chapman SK, Classen AT, Gehring CA, Grady KC, et al. 2014. Plant genetic effects on soils under climate change. *Plant Soil* 379:1–19
- Fordyce JA. 2006. The evolutionary consequences of ecological interactions mediated through phenotypic plasticity. *J. Exp. Biol.* 209:2377–83
- Foster KR, Schluter J, Coyte KZ, Rakoff-Nahoum S. 2017. The evolution of the host microbiome as an ecosystem on a leash. *Nature* 548:43–51
- Gehring CA, Flores-Rentería D, Sthultz CM, Leonard TM, Flores-Rentería L, et al. 2014. Plant genetics and interspecific competitive interactions determine ectomycorrhizal fungal community responses to climate change. *Mol. Ecol.* 23:1379–91
- Gehring CA, Sthultz CM, Flores-Rentería L, Whipple AV, Whitham TG. 2017. Tree genetics defines fungal partner communities that may confer drought tolerance. *PNAS* 114:11169–74
- Gilbert SF, Sapp J, Tauber AI. 2012. A symbiotic view of life: We have never been individuals. *Q. Rev. Biol.* 87:325–41
- Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. 2010. A framework for community interactions under climate change. *Trends Ecol. Evol.* 25:325–31
- Goodnight CJ. 1990a. Experimental studies of community evolution. I. The response to selection at the community level. *Evolution* 44:1614–24
- Goodnight CJ. 1990b. Experimental studies of community evolution. II. The ecological basis of the response to community selection. *Evolution* 44:1625–36
- Goodnight CJ. 1995. Epistasis and the increase in additive genetic variance: implications for phase 1 of Wright's shifting balance process. *Evolution* 49:502–11
- Goodnight CJ. 2000. Heritability at the ecosystem level. *PNAS* 97:9365–66
- Goodnight CJ, Craig DM. 1996. The effect of coexistence on competitive outcome in *Tribolium castaneum* and *Tribolium confusum*. *Evolution* 50:1241–50
- Goodnight CJ, Schwartz JM, Stevens L. 1992. Contextual analysis of models of group selection, soft selection, hard selection, and the evolution of altruism. *Am. Nat.* 140:743–61
- Grady KC, Wood TE, Kolb TE, Hersch-Green E, Shuster SM, et al. 2017. Local biotic adaptation of trees and shrubs to plant neighbors. *Oikos* 126:583–93
- Griffing B. 1967. Selection in reference to biological groups. I. Individual and group selection applied to populations of unordered groups. *Aust. J. Biol. Sci.* 20:127–40
- Herlihy D. 1974. *The Family in Renaissance Italy*. Forums Hist. 125. St. Charles, MO: Forum Press
- Hersch EI, Phillips PC. 2004. Power and potential bias in field studies of natural selection. *Evolution* 58:479–85
- Hubbell SP. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton Univ. Press
- Hubbell SP. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* 19:166–72
- Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M. 2008. Ecological consequences of genetic diversity. *Ecol. Lett.* 11:609–23
- Janzen DH. 1980. When is it coevolution? *Evolution* 34:611–12

- Johnson MTJ, Stinchcombe JR. 2007. An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.* 780:1–8
- Keith AR, Bailey JK, Lau MK, Whitham TG. 2017. Genetics-based interactions of foundation species affect community diversity, stability, and network structure. *Proc. R. Soc. B* 284:20162703
- Keith AR, Bailey JK, Whitham TG. 2010. A genetic basis to community repeatability and stability. *Ecology* 11:3398–406
- Lamit LJ, Busby PE, Lau MK, Compson ZG, Wojtowicz T, et al. 2015a. Tree genotype mediates covariance among diverse communities from microbes to arthropods. *J. Ecol.* 103:840–50
- Lamit LJ, Holeski LM, Flores-Rentería L, Whitham TG, Gehring CA. 2016. Tree genotype influences ectomycorrhizal fungal community structure: ecological and evolutionary implications. *Fungal Ecol.* 24:124–34
- Lamit LJ, Lau MK, Reese Næsborg R, Wojtowicz T, Whitham TG, Gehring CA. 2015b. Genotype variation in bark texture drives lichen community assembly across multiple environments. *Ecology* 96:960–71
- Lamit LJ, Lau MK, Sthultz CM, Wooley SC, Whitham TG, Gehring CA. 2014. Tree genotype and genetically-based growth traits structure twig endophyte communities. *Am. J. Bot.* 101:467–78
- Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–26
- Lau MK, Keith AR, Borrett SR, Shuster SM, Whitham TG. 2016. Genotypic variation in foundation species generates network structure that may drive community dynamics and evolution. *Ecology* 97:733–42
- LCR-MSCP. 2004. *Lower Colorado River Multi-Species Conservation Program*, Vol. 2: *habitat conservation plan*. Final Rep., LCR-MSCP, Sacramento, CA
- Levin SA, Sege LA, Adler FR. 1990. Diffuse coevolution in plant–herbivore communities. *Theor. Popul. Biol.* 37:171–91
- Lewontin RC. 1970. The units of selection. *Annu. Rev. Ecol. Syst.* 1:1–18
- Lynch M, Walsh B. 1998. *Genetics and Analysis of Quantitative Traits*. Sunderland, MA: Sinauer
- Minchin PR. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107
- Mopper S. 1996. Adaptive genetic structure in phytophagous insect populations. *Trends Ecol. Evol.* 11:235–38
- Mopper S, Stiling P, Landau K, Simberloff D, Van Zant P. 2000. Spatiotemporal variation in leafminer population structure and adaptation to individual oak trees. *Ecology* 81:1577–87
- Moran NA, Sloan DB. 2015. The hologenome concept: helpful or hollow? *PLOS Biol.* 13:e1002311
- Mueller RC, Scudder CM, Porter ME, Trotter RT, Gehring CA, Whitham TG. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *J. Ecol.* 93:1085–93
- Neuhausser C, Andow DA, Heimpel GE, May G, Shaw RG, Wagenius S. 2003. Community genetics: expanding the synthesis of ecology and genetics. *Ecology* 84:545–58
- Ostry M, McNabb H. 1985. Susceptibility of *Populus* species and hybrids to disease in the north central United States. *Plant Dis.* 69:755–57
- Patterson A, Flores-Rentería L, Whipple A, Whitham TG, Gehring CA. 2019. Common garden experiments disentangle plant genetic and environmental contributions to ectomycorrhizal fungal community structure. *New Phytol.* 221:493–502
- Price GR. 1972. Extension of covariance selection mathematics. *Ann. Hum. Genet.* 35:485–90
- Queller DC. 2014. Joint phenotypes, evolutionary conflict and the fundamental theorem of natural selection. *Philos. Trans. R. Soc. B* 369:20130423
- Rausher MD. 1996. Genetic analysis of coevolution between plants and their natural enemies. *Trends Genet.* 12:212–17
- Ricklefs RE. 2008. Disintegration of the ecological community. *Am. Nat.* 172:741–50
- Robertson A. 1957. Optimum group size in progeny testing and family selection. *Biometric* 13:442–50
- Roughgarden J, Gilbert SF, Rosenberg E, Zilber-Rosenberg I, Lloyd EA. 2017. Holobionts as units of selection and a model of their population dynamics and evolution. *Biol. Theor.* 13:44–65
- Schweitzer JA, Bailey JK, Fischer DG, LeRoy CJ, Lonsdorf EV, et al. 2008. Plant–soil microorganism interactions: a heritable relationship between plant genotype and associated soil microorganisms. *Ecology* 89:773–81
- Schweitzer JA, Bailey JK, Fischer DG, LeRoy CJ, Whitham TG, Hart SC. 2012. Functional and heritable consequences of plant genotype on community composition and ecosystem processes. In *Trait-Mediated*

- Indirect Interactions: Ecological and Evolutionary Perspectives*, ed. T Ohgushi, O Schmitz, RD Holt, pp. 371–90. Cambridge, UK: Cambridge Univ. Press
- Shuster SM, Lonsdorf EV, Wimp GM, Bailey JK, Whitham TG. 2006. Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution* 60:991–1003
- Simmonds NW. 1996. Yields of cereal grain and protein. *Exp. Agric.* 32:351–56
- Smith DS, Bailey JK, Shuster SM, Whitham TG. 2011. A geographic mosaic of trophic interactions and selection: trees, aphids and birds. *J. Evol. Biol.* 24:422–29
- Smith DS, Lau MK, Jacobs R, Monroy JA, Shuster SM, Whitham TG. 2015. Rapid plant evolution in the presence of an introduced species alters community composition. *Oecologia* 179:563–72
- Stevens L, Goodnight CJ, Kalisz S. 1995. Multilevel selection in natural populations of *Impatiens capensis*. *Am. Nat.* 145:513–26
- Stultz CM, Gehring CA, Whitham TG. 2009a. Deadly combination of genes and drought: increased mortality of herbivore-resistant trees in a foundation species. *Glob. Change Biol.* 15:1949–61
- Stultz CM, Whitham TG, Kennedy K, Deckert R, Gehring CA. 2009b. Genetically-based susceptibility to herbivory influences the ectomycorrhizal fungal communities of a foundation tree species. *New Phytol.* 184:657–67
- Stone AC, Gehring CA, Cobb NS, Whitham TG. 2018. Genetic-based susceptibility of a foundation tree to herbivory interacts with climate to influence arthropod community composition, diversity and resilience. *Front. Plant Sci.* 9:1831
- Strauss SY, Irwin RE. 2004. Ecological and evolutionary consequence of multispecies plant-animal interactions. *Annu. Rev. Ecol. Syst.* 21:435–66
- Swenson W, Arendt J, Wilson DS. 2000a. Artificial selection of microbial ecosystems for 3-chloroaniline biodegradation. *Environ. Microbiol.* 2:564–71
- Swenson W, Wilson DS, Elias R. 2000b. Artificial ecosystem selection. *PNAS* 97:9110–14
- terHorst CP, Zee PC, Heath KD, Miller TE, Pastore AI, et al. 2018. Evolution in a community context: trait responses to multiple species interactions. *Am. Nat.* 191:368–80
- Thompson JN. 1994. *The Coevolutionary Process*. Chicago: Univ. Chicago Press
- Turkington R, Harper JL. 1979. The growth, distribution and neighbor relationships of *Trifolium repens* in a permanent pasture. IV. Fine-scale biotic differentiation. *J. Ecol.* 76:245–54
- Wade MJ. 1977. An experimental study of group selection. *Evolution* 31:134–53
- Wade MJ. 1978. A critical review of the models of group selection. *Q. Rev. Biol.* 53:101–14
- Wade MJ. 1985. Soft selection, hard selection, kin selection, and group selection. *Am. Nat.* 125:61–73
- Wade MJ. 2007. The co-evolutionary genetics of ecological communities. *Nat. Rev. Genet.* 8:185–95
- Wade MJ. 2016. *Adaptation in Metapopulations: How Interaction Changes Evolution*. Chicago: Univ. Chicago Press
- Wade MJ, Bijma P, Ellen ED, Muir W. 2010. Group selection and social evolution in domesticated animals. *Evol. Appl.* 3:453–65
- Wade MJ, Shuster SM. 2004. Sexual selection: harem size and the variance in male reproductive success. *Am. Nat.* 164:E83–89
- Ware IM, Fitzpatrick CR, Senthilnathan A, Bayliss SLJ, Beals KK, et al. 2019. Feedbacks link ecosystem ecology and evolution across spatial and temporal scales: empirical evidence and future directions. *Funct. Ecol.* 33:31–42
- Weber MG, Wagner CE, Best RJ, Matthews B. 2017. Evolution in a community context: on integrating ecological interactions and macroevolution. *Trends Ecol. Evol.* 32:291–304
- West-Eberhard MJ. 1989. Phenotypic plasticity and the origin of diversity. *Annu. Rev. Ecol. Syst.* 20:249–78
- Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* 7:510–23
- Whitham TG, Difazio SP, Schweitzer JA, Shuster SM, Allen GJ, et al. 2008. Extending genomics to natural communities and ecosystems. *Science* 320:492–95
- Whitham TG, Gehring CA, Bothwell HM, Cooper HF, Hull JB, et al. 2020. Using the Southwest Experimental Garden Array to enhance riparian restoration in response to global change: identifying and deploying genotypes and populations for current and future environments. In *Riparian Research and Management: Past, Present, Future*, Vol. 2, ed. SW Carothers, RR Johnson, DM Finch, KJ Kingsley, RH Hamre,

- pp. 63–79. Gen. Tech. Rep. RMRS-GTR-411. Fort Collins, CO: U.S. Dep. Agric. For. Serv. Rocky Mt. Res. Stn
- Whitham TG, Gehring CA, Lamit LJ, Wojtowicz T, Evans LM, et al. 2012. Community specificity: life and afterlife effects of genes. *Trends Plant Sci.* 17:271–81
- Whitham TG, Young WP, Martinsen GD, Gehring CA, Schweitzer JA, et al. 2003. Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84:559–73
- Williams AP, Cook ER, Smerdon JE, Cook BI, Abatzoglou JT, et al. 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. *Science* 368:314–18
- Williams GC. 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton Univ. Press
- Williams HTP, Lenton TM. 2007. Artificial selection of simulated microbial ecosystems. *PNAS* 104:8918–23
- Wilson DS. 1975. A theory of group selection. *PNAS* 72:143–46
- Wilson DS. 1983. The group selection controversy: history and current status. *Annu. Rev. Ecol. Syst.* 14:159–87
- Wilson DS. 1997. Biological communities as functionally organized units. *Ecology* 78:2018–24
- Wilson DS. 2016. Two meanings of complex adaptive systems. In *Complexity and Evolution: Toward a New Synthesis for Economics*, ed. DS Wilson, A Kirman, pp. 31–46. Cambridge, MA: MIT Press
- Wimp GM, Young WP, Woolbright SA, Martinsen GD, Keim P, Whitham TG. 2004. Conserving plant genetic diversity for dependent animal communities. *Ecol. Lett.* 7:776–80
- Zilber-Rosenberg I, Rosenberg E. 2008. Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. *FEMS Microbiol. Rev.* 2008:32:723–35
- Zytynska SE, Fay MF, Penney D, Preziosi RF. 2011. Genetic variation in a tropical tree species influences the associated epiphytic plant and invertebrate communities in a complex forest ecosystem. *Philos. Trans. R. Soc. B* 366:1329–36
- Zytynska SE, Khudr MS, Harris E, Preziosi RF. 2012. Genetic effects of tank-forming bromeliads on the associated invertebrate community in a tropic forest system. *Oecologia* 170:46775



Contents

Arthropod Origins: Integrating Paleontological and Molecular Evidence <i>Gregory D. Edgecombe</i>	1
Diversification of Neotropical Freshwater Fishes <i>James S. Albert, Victor A. Tagliacollo, and Fernando Dagosta</i>	27
Resolving Food-Web Structure <i>Robert M. Pringle and Matthew C. Hutchinson</i>	55
Hedgerows as Ecosystems: Service Delivery, Management, and Restoration <i>Ian Montgomery, Tancredi Caruso, and Neil Reid</i>	81
What We Don't Know About Diet-Breadth Evolution in Herbivorous Insects <i>Nate B. Hardy, Chloe Kaczvinsky, Gwendolyn Bird, and Benjamin B. Normark</i>	103
Extending Plant Defense Theory to Seeds <i>James W. Dalling, Adam S. Davis, A. Elizabeth Arnold, Carolina Sarmiento, and Paul-Camilo Zalamea</i>	123
Origin and Evolution of the Turtle Body Plan <i>Tyler R. Lyson and Gabriel S. Bever</i>	143
Our Current Understanding of Commensalism <i>Kaitlyn A. Mathis and Judith L. Bronstein</i>	167
Evolutionary Dynamics and Consequences of Parthenogenesis in Vertebrates <i>Matthew K. Fujita, Sonal Singhal, Tuliana O. Brunes, and Jose A. Maldonado</i>	191
Ecological Interactions and Macroevolution: A New Field with Old Roots <i>David H. Hembry and Marjorie G. Weber</i>	215
Genomic Prediction of (Mal)Adaptation Across Current and Future Climatic Landscapes <i>Thibaut Capblancq, Matthew C. Fitzpatrick, Rachael A. Bay, Moises Exposito-Alonso, and Stephen R. Keller</i>	245

Food Webs and Ecosystems: Linking Species Interactions to the Carbon Cycle <i>Oswald J. Schmitz and Shawn J. Leroux</i>	271
Ecology and Neurobiology of Fear in Free-Living Wildlife <i>Liana Y. Zanette and Michael Clinchy</i>	297
Predator Effects on Plant-Pollinator Interactions, Plant Reproduction, Mating Systems, and Evolution <i>Amanda D. Benoit and Susan Kalisz</i>	319
What Do We Really Know About Adaptation at Range Edges? <i>Amy L. Angert, Megan G. Bontrager, and Jon Ågren</i>	341
The Floral Microbiome: Plant, Pollinator, and Microbial Perspectives <i>Rachel L. Vannette</i>	363
Parallelism in Flower Evolution and Development <i>Carolyn A. Wessinger and Lena C. Hileman</i>	387
The Evolution of Mutualistic Dependence <i>Guillaume Chomicki, E. Toby Kiers, and Susanne S. Renner</i>	409
The Structure of Ecological Networks Across Levels of Organization <i>Paulo R. Guimarães Jr.</i>	433
The Evolution of Annual and Perennial Plant Life Histories: Ecological Correlates and Genetic Mechanisms <i>Jannice Friedman</i>	461
The Rules of Attraction: The Necessary Role of Animal Cognition in Explaining Conservation Failures and Successes <i>Alison L. Greggor, Oded Berger-Tal, and Daniel T. Blumstein</i>	483
Gene Drive Dynamics in Natural Populations: The Importance of Density Dependence, Space, and Sex <i>Sumit Dhole, Alun L. Lloyd, and Fred Gould</i>	505
Avian Diversity: Speciation, Macroevolution, and Ecological Function <i>Joseph A. Tobias, Jente Ottenburghs, and Alex L. Pigot</i>	533
Climate Disruption of Plant-Microbe Interactions <i>Jennifer A. Rudgers, Michelle E. Afkhami, Lukas Bell-Dereske, Y. Anny Chung, Kerri M. Crawford, Stephanie N. Kivlin, Michael A. Mann, and Martin A. Nuñez</i>	561
Intraspecific Genetic Variation and Species Interactions Contribute to Community Evolution <i>Thomas G. Whitham, Gerard J. Allan, Hillary F. Cooper, and Stephen M. Shuster</i>	587