

COMMUNITY AND ECOSYSTEM GENETICS: A CONSEQUENCE OF THE EXTENDED PHENOTYPE

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Abstract. We present evidence that the heritable genetic variation within individual species, especially dominant and keystone species, has community and ecosystem consequences. These consequences represent *extended phenotypes*, i.e., the effects of genes at levels higher than the population. Using diverse examples from microbes to vertebrates, we demonstrate that the extended phenotype can be traced from the individuals possessing the trait, to the community, and to ecosystem processes such as leaf litter decomposition and N mineralization. In our development of a community genetics perspective, we focus on intraspecific genetic variation because the extended phenotypes of these genes can be passed from one generation to the next, which provides a mechanism for heritability. In support of this view, common-garden experiments using synthetic crosses of a dominant tree show that their progeny tend to support arthropod communities that resemble those of their parents. We also argue that the combined interactions of extended phenotypes contribute to the among-community variance in the traits of individuals within communities. The genetic factors underlying this among-community variance in trait expression, particularly those involving genetic interactions among species, constitute *community heritability*. These findings have diverse implications. (1) They provide a genetic framework for understanding community structure and ecosystem processes. The effects of extended phenotypes at these higher levels need not be diffuse; they may be direct or may act in relatively few steps, which enhances our ability to detect and predict their effects. (2) From a conservation perspective, we introduce the concept of the minimum viable interacting population (MVIP), which represents the size of a population needed to maintain genetic diversity at levels required by *other* interacting species in the community. (3) Genotype \times environment interactions in dominant and keystone species can shift extended phenotypes to have unexpected consequences at community and ecosystem levels, an issue that is especially important as it relates to global change. (4) Documenting community heritability justifies a community genetics perspective and is an essential first step in demonstrating community evolution. (5) Community genetics requires and promotes an integrative approach, from genes to ecosystems, that is necessary for the marriage of ecology and genetics. Few studies span from genes to ecosystems, but such integration is probably essential for understanding the natural world.

Key words: *community evolution; community genetics; community heritability; dominant species; ecosystems; extended phenotype; genetic variation; keystone species; minimum viable interacting population.*

INTRODUCTION

Population genetics is defined as “the study of how Mendel’s laws and other genetic principles apply to entire populations” (Hartl 1980). Community genetics extends these same principles to the more complex arena of communities and ecosystems. Jim Collins (cited in Antonovics 1992) argued for a new discipline called

“community genetics,” which emphasizes “the analysis of evolutionary genetic processes that occur among interacting populations in communities.” This definition allows us to examine complex genetic interactions among diverse organisms and their potential ecosystem consequences (Loehle and Pechmann 1988), but is not dependent upon the reciprocity of coevolution (Antonovics 1992). Our development of community genetics focuses on the role of intraspecific genetic variation in dominant and keystone species, which in turn affects dependent species, community organization, and ecosystem dynamics. Where population ge-

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TABLE 1. Summary of working definitions used in this paper.

Term	Definition	Source
Community	"An association of interacting species living in a particular area"	Molles (1999)
Community evolution	Natural selection leading to phenotypic change at the community level	sensu Wilson (1997)
Community genetics	The role of intraspecific genetic variation in affecting community organization and ecosystem dynamics	Antonovics (1992); this paper
Community heritability	"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."	Goodnight (1990a)
Dominant species	Species that "dominate community biomass and have total impacts that are large, but not disproportionate to their biomass"	Power et al. (1996)
Extended phenotype Intraspecific genetic variation	The effects of genes at levels higher than the population Genetic variation found within a species or hybridizing complex (the largest unit with significant gene flow and heritable transmission of traits from one generation to the next)	Sensu Dawkins (1982) this paper
Keystone species	A species "whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance"	Power et al. (1996)
Minimum Viable Interacting Population (MVIP)	The size of a population needed to maintain genetic diversity at levels required by other interacting species in the community	this paper

netics considers the phenotype to be the expression of genes in individuals and populations, from a community perspective, we define the extended phenotype (sensu Dawkins 1982) as the effects of genes at levels higher than the population. Because these extended phenotypes can be heritable, here we explore their community, ecosystem, and evolutionary consequences (see Table 1 for a summary of working definitions used throughout this paper).

Why add complexity to the already complex field of population genetics? Community genetics recognizes the simple, but messy, truth that organisms do not live in a vacuum. Most species have evolved and live within a matrix of interactions that encompass 100s, if not 1000s, of species in a changing physical environment. Understanding how species fit into this matrix is essential to our basic comprehension of how the larger system works. For example, van Ommeren and Whitham (2002) showed that if we examine the relationship between mistletoe and junipers as a simple two-way interaction, the relationship is parasitic. If, however, we include their seed-dispersing birds in a three-way interaction, mistletoe can be a mutualist of juniper. Thus, adding just one additional species to the matrix of interactions can potentially reverse our basic conclusions (see also Orians and Fritz 1996). Such reversals in outcomes emphasize the need to include more factors if we are to understand Darwin's "tangled bank."

Community genetics embraces the complexity of the natural world to understand the consequences of genetic variation, multiple trophic levels, and complex interactions with the environment. Our perspective argues that community genetics is an emerging and important field for understanding our natural world. It is

the process of scaling up to understand the higher level consequences of genes on communities and ecosystems. The goal of this paper is to examine how the extended phenotypes of genes have important consequences at community and ecosystem levels. We first develop the genetic mechanisms of the extended phenotype and argue that their community consequences are heritable. Because genes pass from generation to generation within a species, not among species, we concentrate on the genetic variation within an individual species or hybridizing complex. We develop a series of empirical studies emphasizing how extended phenotypes are most likely to be expressed in dominant or keystone species, how their effects are broadly distributed across diverse taxa from microbes to vertebrates, how their expression is influenced by the environment, and how they are important for conservation. We conclude by exploring community evolution, the ultimate consequence of heritable extended phenotypes.

IMPORTANCE OF STUDYING INTRASPECIFIC GENETIC VARIATION

Why do we need an intraspecific genetic variation perspective when ecologists are unable to agree that individual species or species diversity matter in communities and ecosystems (e.g., Schwartz et al. 2000, Diaz and Cabido 2001)? We argue that species do matter and that the genetic variation within species is important for two major reasons. (1) The transmission of traits from one generation to the next occurs within species, not among species (microbes are notorious exceptions). For this reason, to understand the genetic basis of extended phenotypes and their evolutionary consequences, we concentrate on genetic variation within species and hybridizing complexes where there

is significant gene flow. (2) Only by partitioning total genetic variation into three classes (within populations, among populations within species, and among species) can we determine the portion of total genetic variation that covaries among species. Thus, to understand interactions among species and communities, we must first concentrate on the genetic variation within species. In combination, these two points argue that an intraspecific perspective provides a mechanistic basis for understanding the ecological and evolutionary consequences of extended phenotypes.

Community genetics integrates ecology and genetics by studying the genetic traits responsible for the species interactions that create communities. Species interactions are influenced by extended phenotypes, and these interactions can be positive, neutral, or negative. Such interactions among species have been shown to contribute to the among-community component of phenotypic variance, a characteristic defined as community heritability (Goodnight 1990*a, b*, Goodnight and Craig 1996; see also Wade 1977). Laboratory studies on simple, two-species communities demonstrate that an among-community component of variance can arise within just five generations (Goodnight 1990*a, b*, Goodnight and Craig 1996). Selection on individuals within communities evidently favored particular genetic interactions that, when community-level selection was imposed, were passed intact from “parent” to “offspring” communities. In more complex communities, similar genetic interactions are likely to arise and contribute to community heritability (Swenson et al. 2000).

In our development of community genetics, it is important to demonstrate that genes affect traits that are likely to have community and ecosystem consequences. Most of these traits are expected to be quantitative, meaning that they are determined by multiple genetic and environmental factors (Lynch and Walsh 1998). The transmission of these factors from parents to offspring provides the heritable, and thus selectable, variation for these traits in a population. Simple heritability estimates provide the first step in linking a trait to species interactions within communities. More precise estimates about the genetic factors responsible for these complex traits can be obtained with genetic mapping techniques and Quantitative Trait Locus (QTL) analysis. QTL analysis detects a chromosomal region containing one or more loci that affect a trait in a specific environment and can be used to estimate the number of genes involved, magnitude and sign of their effect (+ or –), mode of gene action (additive, dominant), and gene interactions (epistasis). A detailed understanding of individual genes, including their gene frequencies and the magnitude of their effects on the trait, is essential for understanding the genetic basis of quantitative variation (Falconer and Mackay 1996). This is important because genetic variation resulting from a few genes of large effect will produce a sig-

nificantly different response to selection than a large number of genes of small effect (Lynch and Walsh 1998), and can significantly alter an extended phenotype and the resulting interactions. Recent theory suggests that quantitative traits are determined by a combination of a few loci of large effect and many loci of small effect, with a significant portion of the variation being determined by the loci of large effect (reviewed in Mackay 2001; but see Wolf et al. 1998, Wade 2002). We will focus on genes of large effect because the introduction of these genes through mutation or gene flow from other populations could significantly alter an extended phenotype, resulting in drastic changes in community structure. Understanding genetic architecture can also reveal the presence of + or – genetic correlations among traits (Hawthorne and Via 2001), which can cause rapid evolutionary responses in a species (Widmer 2002). In the future, technological advances in bioinformatics and genomics may allow the analysis of the actual genes or alleles that affect species interactions, greatly increasing our precision in mapping these effects.

The potential for these molecular approaches to facilitate a community genetics perspective is illustrated by QTL analyses that have quantified the genetic basis of ecologically important traits in plants (Alonso-Blanco et al. 1998, Kim and Rieseberg 1999), invertebrates (Page et al. 2000), and vertebrates (Robison et al. 2001). Genes of large effect that could have community and ecosystem consequences have been identified in QTL as being responsible for bud set and flush (Frewen et al. 2000), tree growth and architecture (Bradshaw and Stettler 1995), pathogen resistance (Newcombe and Bradshaw 1996), and chemical defenses (Shepherd et al. 1999). In addition, major qualitative phenotypic differences, such as changing a fungus from a pathogen to a mutualist (Freeman and Rodriguez 1993), the number of queen ants tolerated by workers (Krieger and Ross 2002), and trichome morphology (van Dam et al. 1999) are controlled by a single gene.

Key points that emerge from this section include the following: (1) a community genetics perspective is dependent upon an understanding of intraspecific genetic variation, which is the source of heritable genetic variation; (2) laboratory experiments show that genetic interactions between species can be passed from “parent” to “offspring” communities (i.e., community heritability); and (3) QTL and other genetic analyses provide powerful tools for quantifying and mapping the extended phenotypes of genes that have community and ecosystem consequences. The following three sections emphasize studies of dominant and keystone species in the wild because, as community drivers, their intraspecific genetic variation has especially important consequences for understanding community genetics.

GENETIC VARIATION IN DOMINANT SPECIES

Many vegetation types are characterized by a few species that “dominate community biomass and have

total impacts that are large, but not disproportionate to their biomass" (Power et al. 1996). Although all interacting community members are likely to show community genetic effects, the extended phenotypes resulting from genetic variation in these dominant species are likely to have particularly strong effects on the communities in which they are embedded. Such species often exhibit extensive variation in their chemical profiles due to genetics, environment, and genotype \times environment interactions (Denno and McClure 1983, Fritz and Simms 1992, Karban and Baldwin 1997). We show that the genetic variation in dominant species has community consequences and that community composition and richness can be heritable.

Aspen, a dominant tree of early-successional forests throughout much of North America, exhibits extensive genetic variation in its chemical defense system (Lindroth and Hwang 1996, Mitton and Grant 1996). Major secondary metabolites such as condensed tannins and phenolic glycosides may vary 25-fold in concentration (Lindroth et al. 1987, Lindroth and Hwang 1996). Field and common-garden studies show that levels of condensed tannins are highly variable among genotypes, and vary greatly with resource availability (e.g., light, nutrients) and defoliation (Hwang and Lindroth 1997, Osier et al. 2000, Osier and Lindroth 2001). In contrast, the same studies show that levels of phenolic glycosides exhibit marked genetic variation but minimal environmental variation.

The extended phenotypes of these secondary metabolites influence interactions between aspen, herbivores, and higher trophic levels. Phenolic glycosides provide resistance against insects, pathogens, and mammals (Lindroth and Hwang 1996). When gypsy moths (*Lymantria dispar*), major defoliators, were reared on different aspen genotypes, survival rates ranged from 0% to 100%. The same compounds affect the viability of the pathogen *Hypoxyton mammatum*, as well as feeding by snowshoe hares (*Lepus americanus*). Higher trophic levels are also affected. Holton (2001) found that survivorship and growth of the parasitoid *Compsilura concinnata*, reared in forest tent caterpillars, varied two-fold among aspen genotypes upon which the caterpillars fed. The adult mass of these parasitoids was negatively correlated with levels of phenolic glycosides in the diet of their hosts, indicating that the genetic-based effects of chemical variation in aspen were extended to the enemies of its enemy.

A plant's extended phenotype of the community of organisms that it supports can be just as predictable as the plant's own "traditional" phenotype of morphological traits. Floate and Whitham (1995) classified individual trees as *Populus fremontii*, F_1 hybrids between *P. fremontii* and *P. angustifolia*, and complex backcrosses, based upon two data sets collected from the same trees. They found that when trees were classified based upon their own morphological traits or their arthropod communities, there was a 98% level of agree-

ment. Thus, in this field study, the arthropod community was just as good a predictor of a tree's taxonomic status as its own morphological traits. This finding argues that the underlying genotype of a dominant plant produces an extended phenotype that is reflected at the community level. Studies of other hybridizing systems including willows (Fritz and Price 1988), sagebrush (Messina et al. 1996), and oaks (Aguilar and Boecklen 1992) also demonstrate community-level consequences of genetic variation (see review by Whitham et al. [1999]).

Studies of *Eucalyptus* in Australia observationally and experimentally show that the extended phenotype of community structure is heritable. In the wild, *E. amygdalina* naturally hybridizes with *E. risdonii* at their boundaries to form a hybrid swarm (Potts and Reid 1985). Analyses of insect and fungal taxa on F_1 s, backcross hybrids, and pure parental phenotypes showed that these cross types significantly differed in their communities (Whitham et al. 1994). To separate genetic and environmental hypotheses that might account for these patterns, controlled crosses of *E. amygdalina* and *E. risdonii* produced a synthetic population of known pedigree. Three years after planting, the distributions of 30 insect taxa were quantified.

A major finding of these common-garden trials was that the progeny of these crosses accumulated the insect communities of both parents, suggesting that the genetic factors underlying these plant-insect associations have additive effects (Dungey et al. 2000). Such transmission of extended phenotypes from one community generation to the next is powerful evidence that community structure is heritable. Fig. 1 shows the results obtained using GNMDS (global nonmetric multidimensional scaling) ordination techniques. Each point represents the community of arthropods found on at least three or more trees in each genetic family, and the entire analysis is based upon 953 trees. Because the hybrids accumulated the insect communities of both parental species, the F_1 families were intermediate in ordination space and differed significantly from both parental species. The single F_2 family differed significantly from the parental *E. risdonii* families, but not from the *E. amygdalina* families, which is consistent with the inheritance of quantitative traits. Because common and rare insect species were treated equally, these patterns were not driven by a few common species, but represent community-wide patterns. In agreement with these findings, analyses of the 31 essential oils associated with the defensive chemistry of these trees resulted in similar patterns, i.e., the F_1 hybrids accumulated all the oils of both parental species and were intermediate (Dungey et al. 2000).

These studies demonstrate three points that are fundamental to our view of the extended phenotype: (1) dominant species possess significant genetic variation in their chemical profiles, which affects consumers and their enemies; (2) at a local scale, the extended phe-

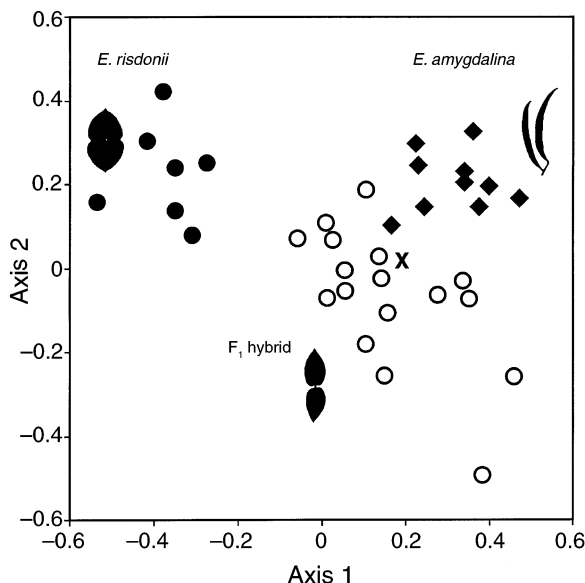


FIG. 1. In common-garden trials using crosses of known pedigree, F_1 hybrids accumulated the arthropod communities of both parental species, suggesting a heritable component to community structure. Each point represents the arthropod community of 30 insect taxa found on a family of trees, based upon a minimum of three trees and a total of 953 trees. *Eucalyptus amygdalina* (diamonds), *E. risdonii* (solid circles), their F_1 hybrids (open circles), and a single family of F_2 hybrids (\times). Findings are based on the first two dimensions (Axis 1 and Axis 2), of a six-dimension global nonmetric multidimensional scaling (GNMDS), and are adapted from Dungey et al. (2000).

notype of a plant (e.g., its dependent community) can be just as predictable as the “traditional” phenotype (e.g., plant morphology) in distinguishing among plant genotypes; and (3) synthetic crosses demonstrate a heritable component to community composition and species richness.

GENETIC VARIATION IN KEYSTONE SPECIES

A keystone species is defined as “one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance” (Power et al. 1996). Because of the disproportionate effects of keystone species and their propensity to interact strongly with a wide range of other species, genetic factors underlying the extended phenotypes of keystone species may have especially strong effects on communities and ecosystems. Thus, those species with the strongest ecological effects are also likely to be those with the strongest community genetic effects.

Pacific salmon are recognized as keystone predators in aquatic and marine communities (Power 1990), and their decomposing bodies are a major source of nutrients in both aquatic and terrestrial systems (Willson and Halupka 1995, Helfield and Naiman 2001). Ecologically important traits that are heritable in salmon include the timing of juvenile and adult migrations,

maturation date (Groot and Margolis 1991, Quinn and Unwin 1993), and reproductive energy allocation (Kinison et al. 2001). Large rivers have genetically differentiated salmon populations that migrate during most months of the year in different tributaries (Groot and Margolis 1991). Genetic variation in the timing of migration and energy allocation to reproduction is likely to cascade to affect the timing and flux of nutrients from the ocean to aquatic and riparian ecosystems.

The importance of salmon-derived nutrient influx has been demonstrated in the riparian Sitka spruce forests of Alaska. Trees along reaches with spawning salmon exhibit three times more growth than trees along reaches without salmon (Helfield and Naiman 2001). In response to the temporal variation in migration and spawning, behavioral changes have occurred in bears, otters, mink, and eagles, which depend upon salmon as a major source of food (Cederholm et al. 1989, Ben-David 1997). Enhanced riparian plant growth derived from the transfer of nutrients to the terrestrial community creates a positive feedback that increases the survival of future salmon generations (Helfield and Naiman 2001).

In another example, the interaction between anthrax (*Bacillus anthracis*) and browsing ungulates in South Africa (K. L. Smith, D. T. Scholl, V. De Vos, H. Bryden, M. E. Hugh-Jones, and P. Keim, *unpublished manuscript*) shows how genetic factors underlying the extended phenotypes of pathogens may shift the balance between woodlands and grasslands. Type B anthrax strain is associated with death rates 15 times higher than Type A. The virulence of these two strains differentially affects 15 species of ungulates in Kruger National Park, which has a history of anthrax outbreaks. In addition to these differences in mortality between strains, browsing ungulates kudu (*Tragelaphus strepsiceros*) and nyala (*T. angasii*) suffer a death rate 10 times greater than ungulates that feed on grasses (K. L. Smith, D. T. Scholl, V. De Vos, H. Bryden, M. E. Hugh-Jones, and P. Keim, *unpublished manuscript*). Because the expansion of woody shrubs (e.g., *Acacia*) often follows outbreaks (Prins et al. 1993), it is likely that anthrax outbreaks promote woodland invasion of grassland. Thus, anthrax outbreaks and the relative abundance of the two anthrax strains may ultimately cause a cycle between woodlands and grasslands. Similar examples of keystone effects in other systems include the bacterium that causes plague (*Yersinia pestis*; Biggins and Kosoy 2001), and fig trees that are resources for vertebrate frugivores (*Ficus* spp.; Janzen 1979).

These examples argue two points: (1) genetic differences underlying the extended phenotypes of keystone species have community and ecosystem consequences; and (2) these effects involve keystone plants, animals, and microbes from marine to terrestrial environments.

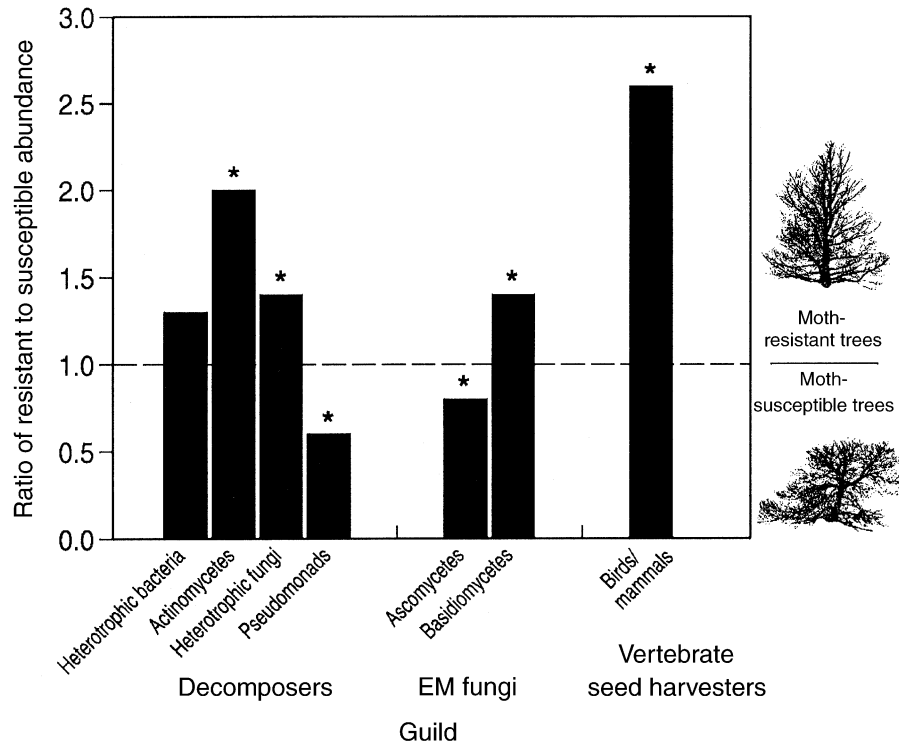


FIG. 2. Genetic variation among pinyon pines (*Pinus edulis*, a community dominant) in resistance to a keystone herbivore (*Dioryctria albiovittella*, a stem-boring moth) affects bird, mammal, and rhizosphere microbe communities. The graph shows the ratio of the abundance of seven guilds on resistant trees relative to susceptible trees. Bars with values >1 indicate greater abundance of a guild on resistant trees than on susceptible trees; bars with values <1 indicate greater abundance on susceptible trees than on resistant trees. An asterisk above the bar denotes a statistically significant difference at $P < 0.05$. Data are adapted from Christensen and Whitham (1993), Brown et al. (2001), and Kuske et al. (2003).

INTERACTIONS OF DOMINANT AND KEYSTONE SPECIES

Because many communities are likely to have interacting dominant and keystone species, the combined effects of their extended phenotypes may be especially important to investigate. For example, pinyon pine, *Pinus edulis*, is a dominant tree of pinyon–juniper woodlands, the third most common vegetation type in the United States. *Pinus edulis* exhibits variation in resistance to a stem-boring moth, *Dioryctria albiovittella*, which has both a genetic and an environmental component (Mopper et al. 1991). Under normal environmental conditions, this insect has little impact on its host, regardless of genotype, but as soil moisture and nutrient stress increase, the insect becomes a cryptic keystone species (Brown et al. 2001). At stressful sites, ~20% of trees are genetically resistant to the moth and suffer little attack, whereas the remaining genetically susceptible trees are chronically attacked. The destruction of terminal shoots of susceptible trees by the moth turns normally upright trees into shrubs and nearly eliminates female cone production (Whitham and Mopper 1985), which, in turn, affects seed-dispersing birds and mammals (Christensen and Whitham 1993) (Fig. 2). In the absence of moths, birds harvest a greater

proportion of the seed crop, potentially dispersing the seeds over long distances (Vanderwall and Balda 1981). However, in the presence of moths, the reduced cone crop leads to greater seed removal by rodents, which disperse seeds over shorter distances (Vanderwall 1997). Thus, resistance to herbivory determines the outcome of competitive interactions among birds and mammals for seeds, which results in an important feedback loop to the tree in its effects on local vs. long-distance seed dispersal.

These genetic differences in herbivore susceptibility also affect a microbial community of ~600 species that is associated with pinyon roots. The abundance of ectomycorrhizal fungal mutualists is 30% lower on moth-susceptible trees than on resistant trees (Gehring and Whitham 1991). Moth-susceptible trees are dominated by members of the fungal subdivision Ascomycotina, whereas resistant trees are dominated by Basidiomycotina (Fig. 2; Brown et al. 2001). Three of four decomposer guilds are also affected. Actinomycetes and heterotrophic fungi are 30–200% more abundant on resistant than susceptible trees, whereas pseudomonads show the opposite pattern, and only heterotrophic bacterial abundance does not differ significantly (Kuske et al. 2003; Fig. 2). These shifts are important because

the structure of the microbial community can affect tree performance and ecosystem processes. Species of ectomycorrhizal fungi vary in drought tolerance and the ability to utilize organic nitrogen (Smith and Read 1997), qualities that affect their positive feedback on the tree. Among the decomposers, actinomycetes degrade recalcitrant substances (McCarthy and Williams 1992), whereas pseudomonads may promote plant growth by competing with pathogens and acting as helpers in mycorrhizal symbioses (Défago and Haas 1990, Garbaye 1994). Thus, the extended phenotypes of moth-resistant and moth-susceptible trees determine the community structure of hundreds of species from microbes to vertebrates.

Genetic differences within a dominant plant species can also affect the formation of keystone mutualisms. For example, host plant genotype determines the presence and strength of the mutualism between aphids and tending ants, which, in turn, affects an arthropod community of >90 species. Genetic differences among cottonwoods (*Populus fremontii*, *P. angustifolia*, F₁ and backcross hybrids) affect the fecundity and distribution of the aphid *Chaitophorus populicola* (Wimp and Whitham 2001). When aphids were transferred onto trees of varying genotype in a common garden, aphid fecundity across cottonwood genotypes differed approximately threefold in just 10 days, an effect that was mirrored in the distribution of aphids at field sites. Given a suitable host genotype, the survival of the aphid colony then depends upon the acquisition of ant mutualists such as *Formica propinqua*. Field observations and experiments showed that if an aphid colony was <5 m from an ant mound, a mutualism would form, but if the distance was >5 m, it would fail and the colony would die out (Wimp and Whitham 2001). *F. propinqua* repels other herbivores, other species of ants, and generalist predators, yet, the mutualism attracts a unique group of predators and parasites with adaptations for cryptic living among aphid-ant mutualists. Because these specialists are found only in association with the ant-aphid mutualism, whereas others are found only in its absence, the greatest species diversity is achieved in an environment that contains a mosaic of tree genotypes in varying proximity to tending ants.

These examples illustrate two points: (1) genetic variation within dominants may be most important when it affects keystone species; and (2) these genetic differences affect the composition and biodiversity of the community (see the *Conservation implications* section).

ENVIRONMENTAL INTERACTIONS

The environments in which the genes of keystone and dominant species are embedded will greatly influence their extended phenotypes and subsequent effects on communities and ecosystems. Genotype \times environment interactions occur when different genotypes vary

in their response to environmental change (Lynch and Walsh 1998). For example, Orians and Fritz (1996) found that under normal conditions, some willow genotypes were two times more resistant to insect herbivores than were other genotypes. However, when fertilizer was added to simulate good environmental conditions, the formerly resistant genotypes became nearly three times more susceptible. Because willows dominate many riparian communities, such reversals in their resistance phenotypes due to an environmental interaction could result in a pronounced shift in the dependent community of organisms.

Genotype \times environment interactions are likely to take on additional significance as humans continue to rapidly modify environments and the genotypes that occur within them (Palumbi 2001). Humans have eliminated and fragmented habitats, introduced exotic species, and altered atmospheric chemistry, which can interact with genes of dominant and keystone species to alter communities. For example, in aspen, genes interact with environmental pollutants to affect multiple trophic levels. Holton (2001) found that the performance of the forest tent caterpillar (*Malacosoma disstria*) did not vary significantly with aspen genotype when exposed to elevated ozone (O₃), but when exposed to the combination of elevated O₃ and CO₂, performance varied 35% among aspen genotypes. This complex interaction has an extended phenotype in which a higher trophic level is affected; performance of the parasitoid (*Compsilura concinnata*) differed threefold among genotypes under elevated O₃ and CO₂.

These anthropogenic-caused environmental changes may lead to unpredictable genotype \times environment interactions whose extended phenotypes dramatically alter communities. The common reed, *Phragmites australis*, was considered rare or uncommon in North America during the 1800s. However, the introduction of an exotic genotype of this species from Europe, Africa, or Asia (Saltonstall 2002), combined with human-caused environmental disturbances (e.g., agricultural drainage, dikes, and urban expansion; Chambers et al. 1999), has led to an expansion of *P. australis*, such that it is a dominant plant species in wetlands throughout the mainland United States and southern Canada. Its increased dominance has resulted in dramatic decreases in the diversity of wetland plant and bird communities (Chambers et al. 1999) and the apparent disappearance of native *P. australis* genotypes from New England (Saltonstall 2002). The fact that an exotic genotype of a native species has such large community consequences emphasizes the importance of intraspecific genetic variation and the extended phenotypes that come about through interactions with the environment.

These studies demonstrate two points: genetic interactions with the environment affect dominant species, whose extended phenotypes can cascade to affect multiple trophic levels; and human activities will probably increase the importance of genotype \times environment

interactions through changes in abiotic (e.g., climate) and biotic (e.g., exotic introductions) environments. A community genetics perspective is important to understand the ramifications of these human impacts on ecosystems.

GENES TO ECOSYSTEMS

Because the extended phenotypes of dominant and keystone species influence communities, the next step is to examine their effects on ecosystem-level processes such as decomposition and nutrient cycling. This provides a genetic and evolutionary framework to ecosystem studies that has rarely been addressed. Treseder and Vitousek (2001) quantified the consequences of genetic variation in *Metrosideros polymorpha* ('ohi'a, Myrtaceae) on ecosystem function in Hawaii. They compared allozyme diversity of functional enzymes in *M. polymorpha* populations along a fertility gradient to determine the genetic distance between populations. Seedlings were collected from each population and were grown in a common garden with reciprocal nutrient treatments to determine if genetic differences were associated with differences in ecosystem function. They concluded that small differences in allelic diversity led to differences in plant traits such as root and leaf litter chemistry, which, in turn, resulted in positive feedbacks that may influence nutrient cycling. Likewise, Madritch and Hunter (2002) found that phenotypic diversity among nine genotypes of *Quercus laevis* had significant impacts on carbon and nitrogen fluxes. They found that litter phenotype, as determined by a genetic distance matrix, was positively related to litter chemistry that affected both litter decomposition and ammonium availability. Across both of these landscapes, the genetic mosaic created by intraspecific variation translated into a mosaic of ecosystem processing. Although these studies demonstrate the existence of a genetic correlate with ecosystem dynamics, the specific genes involved and the traits that they affect are unknown.

Recent studies show that the effects of mapped genes in a dominant plant can be traced to ecosystem-level processes. This approach uses experimental crosses of known pedigree and QTL analyses to establish the genetic basis of specific traits that are probably important to ecosystem function. Using synthetic crosses between *Populus fremontii* and *P. angustifolia*, Woolbright (2001) found that a significant portion of the phenotypic variation in the production of condensed tannins in cottonwood leaves could be accounted for by a single QTL (Fig. 3A). The effects of genetic differences in tannin production are extended to higher levels. Driebe and Whitham (2000) used leaves from the same cross types and found manifold differences in tannin concentrations (Fig. 3B), which subsequently explained 63% of the variation in litter decomposition in an aquatic system (Fig. 3C). Furthermore, stand-level comparisons in the riparian zone demonstrated that the amount

of condensed tannin that entered the stand through annual litterfall better predicted net N mineralization than did total biomass inputs or lignin : N ratios (Fig. 3D; J. A. Schweitzer, S. C. Hart, J. K. Bailey, S. Woolbright, and T. G. Whitham, *unpublished manuscript*). These combined studies in aquatic and terrestrial components of the same system demonstrate the direct links between a mapped trait, leaf litter chemistry, and the ecosystem processes of decomposition and nitrogen mineralization. Knowing that condensed tannins are heritable is of general significance because these compounds influence nutrient cycling in diverse systems (Hattenschwiler and Vitousek 2000) and they deter pathogens and herbivores (Hemingway and Karchesy 1989).

It is also important to consider the indirect links (i.e., interactions that involve a third step or organism) of the condensed tannin QTL. For example, some tree genotypes are highly susceptible to the gall-forming aphid, *Pemphigus betae*, whereas others are highly resistant (Whitham 1989). On genetically susceptible trees, aphids induce a 4–7 fold increase in leaf tannins, which result in 35–45% slower rates of decomposition than in non-galled leaves from the same trees (J. A. Schweitzer, *unpublished data*). Such “afterlife” effects of herbivory (see also Choudhury 1988, Findlay et al. 1996) result when the genes that affect resistance to aphids interact with the genes for tannin production to indirectly affect an ecosystem process. The presence–absence of aphids also affects species richness and the abundance of 42 other taxa including birds, fungi, and arthropods (Dickson and Whitham 1996). The interaction between the genes for condensed tannins and genes for aphid resistance results in indirect effects that may exceed the direct effects.

Other studies also suggest that intraspecific genetic variation and complex interactions are common and important. Genetic differences in plant chemistry (Nichols-Orians et al. 1993, Adler et al. 1995, Lindroth et al. 2001), physiological processes (i.e., carbon uptake, water use efficiency, resilience to changing environments; Bassman and Zwier [1991], Osorio and Pereira [1994], Benowicz et al. [2001]), and pest resistance (Fritz and Price 1988, van Dam and Vrieling 1994, Orians and Fritz 1996) suggest that extended phenotypes exist for numerous plant traits.

These studies emphasize two points: (1) when acting through a dominant species, genes such as the QTL for tannins have extended phenotypes that have ecosystem consequences; and (2) these effects need not be diffuse; they can be direct or act in relatively few steps to affect ecosystem processes (e.g., the QTL for leaf tannins affect decomposition and N mineralization).

CONSERVATION IMPLICATIONS

Although it has long been recognized that to save a species we need to conserve its genetic diversity, the importance of its genetic diversity for the rest of the

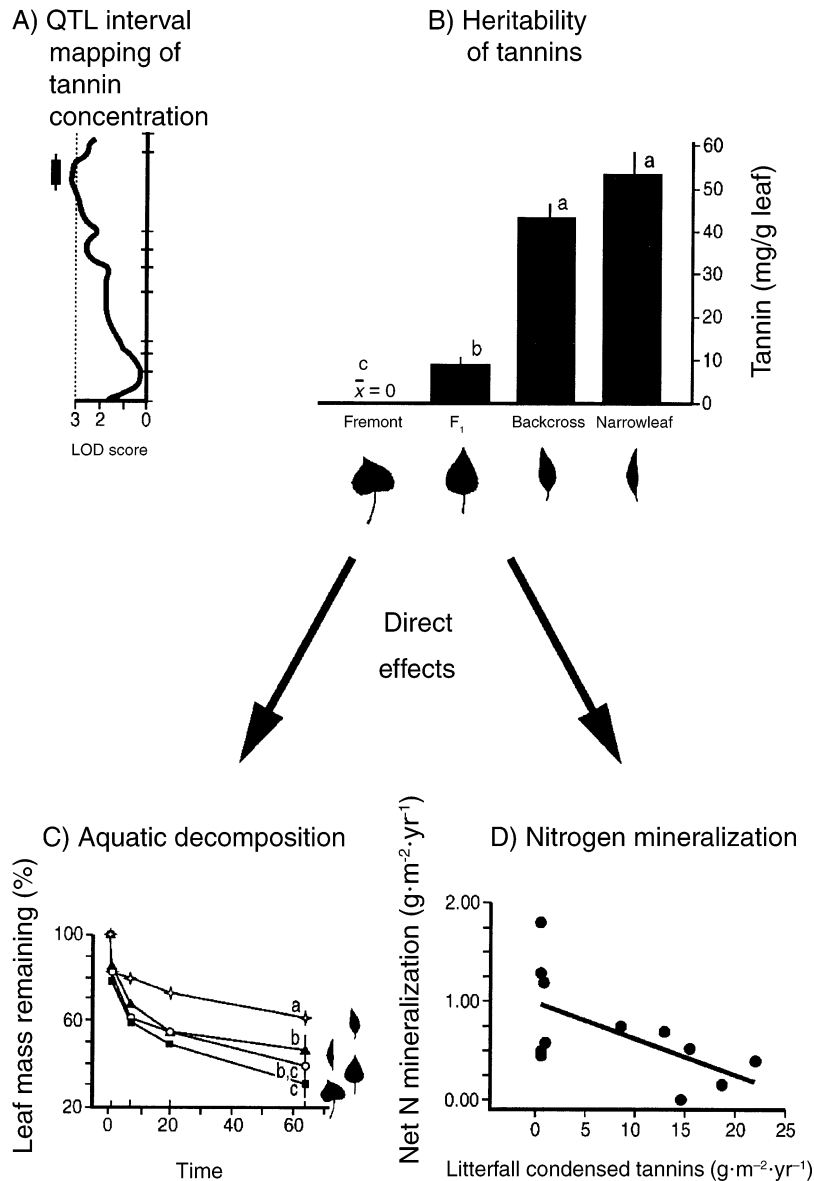


FIG. 3. Genetic variation in *Populus* hybrids results in differential expression of a condensed tannin QTL (Quantitative Trait Locus) that can be traced through ecosystem-level processes. (A) Composite interval mapping shows the location of a QTL for tannin concentration on a linkage group of a *Populus fremontii* × *P. augustifolia* backcross family. One or more genes that influence tannin production are located in the region where the significance threshold level exceeds LOD 3.0 (log of the difference, equivalent to $P < 0.001$; Woolbright 2001). (B) In a common environment, these cross types express manifold differences in the concentration of condensed tannins (Driebe and Whitham 2000). (C) The concentration of condensed tannins in different *Populus* cross types accounts for 63% of the variation in litter decomposition among cross types in a stream (Driebe and Whitham 2000). For panels (B) and (C), vertical lines represent 1 SE, and different letters indicate significant differences among means ($P < 0.05$). (D) The concentration of condensed tannins also explains 57% of the variation in terrestrial net N mineralization rates between 12 stands that differ in cross type compositions (Schweitzer, unpublished manuscript).

community has been much less appreciated. If individual species are dependent upon a subset of the genome of another species, then their survival is more closely tied to conserving the individuals possessing those specific genes rather than all individuals in the other species' population. A consequence of the extended phenotype is that conservation genetics must

include another dimension that recognizes the importance of genes in one species to other dependent species.

An example of one species being dependent upon the genetic makeup of another species is that of the gall mite, *Aceria parapopuli*, on cottonwoods. McIntyre and Whitham (2003) found that 99.9% of the

mite's population was concentrated on naturally occurring F_1 hybrids. In five years of common-garden trials, genetic differences among trees in the "potential" host population resulted in vastly different growth rates of mites, in which the intrinsic rate of increase (r) ranged from 0 to 1.5 on individual tree genotypes. Because suitable F_1 hybrid hosts are rare in the wild, the "actual" host population for these mites is a small subset of the larger cottonwood population. Even though cottonwoods are dominant trees in riparian forests, a dependent species can still be host limited.

Even generalist species can be genetically differentiated and highly specialized at the local level (Thompson 1994). The eastern tiger swallowtail, *Papilio glaucus*, has a large list of host species, but at a local scale, it can be very host specific (Scriber 1986). Other examples are provided by Feder et al. (1988), Wood and Keese (1990), Roinen et al. (1993), and Thompson (1994). Microbes can exhibit even greater specificity. Gene-specific interactions between *Rhizobium leguminosarum* bv. *viciae* and native Afghani pea plants (*Pisum sativum*) regulate symbiosis. The loss of a single gene will disrupt the symbiotic interaction and prevent nitrogen fixation (Vijn et al. 1993).

Such specificity suggests that minimum viable population (MVP) sizes (Shaffer 1981) in one species may be too small to support important interactions with other species (see Thompson 1994). Other researchers have recognized the weaknesses associated with conservation of individual species rather than communities or ecosystems (e.g., Rohlf 1991, Simberloff 1998). Community genetics provides a mechanism to support these criticisms, and furthers the argument against single-species management.

Because of these concerns, we propose a minimum viable interacting population size (MVIP) that represents the size of a population needed to maintain the genetic diversity at levels required by other dependent and interacting species. Minimum viable population (MVP) sizes for conserving the target species are probably much smaller than what is required to conserve other dependent community members, the MVIP. Thus, MVP represents the lower end that is required to conserve the species, and MVIP represents the upper end that is required to conserve community interactions that are important for dependent species. These end points should serve as a guide for future conservation efforts and provide a mechanism for why conservation efforts may flounder if they do not consider the community consequences of genetic variation in dominant and keystone species. Additionally, although current conservation strategies target rare species, it may be just as important to conserve the genetic variation in dominant and keystone species, because their extended phenotypes affect the rest of the community.

The preceding arguments emphasize four points: (1) because of their extended phenotypes, it is important to conserve genetic diversity in dominant and keystone

species; (2) single-species management may fail to preserve crucial interactions upon which other community members are dependent; (3) an understanding of community genetics should broaden conservation goals because genetic variation is linked not just to single-species survival, but also to patterns of interactions among species; and (4) minimum viable interacting population (MVIP) size better reflects goals to conserve interactions and their dependent species.

MULTILEVEL SELECTION AND COMMUNITY EVOLUTION

Evolutionary change results when selection acts on heritable characters. We have argued that selection on genetic factors underlying extended phenotypes can lead to community evolution. As evidence of this process, we have cited research on laboratory populations in which genetically based interactions among species contribute to the among-community component of phenotypic variance, that is, to *community heritability* (Goodnight 1990a, b, Goodnight and Craig 1996, Swenson et al. 2000; see also Wade 1977). We have shown that the genotypes of successive generations of trees in *Eucalyptus* populations of known pedigree predictably affect the composition and richness of their resident insect communities (Dungey et al. 2000). Thus, "offspring" communities of insects on *Eucalyptus* trees resemble the "parent" communities that produced them, direct evidence that community heritability exists. Although the examples that we cite focus on genetic factors underlying the extended phenotypes of dominant and keystone species, genetic interactions between extended phenotypes and their associated species contribute to community heritability. These interactions ultimately lead to genetically distinct communities, whose differences are detectable as the among-community component of variance in individual trait expression.

To understand the broader significance of community evolution, it is necessary to show that, under natural conditions, selection acts on genetic differences *at the community level*. Much of the controversy over the importance of multilevel selection arises from an historical emphasis on circumstances in which the effects of group and higher level selection *supersede* those of individual selection (Williams 1966). This approach presents an extreme case. It ignores circumstances in which the effects of group and higher level selection, as well as interactions among these levels, significantly influence individual relative fitness. Quantitative methods for identifying group and higher level effects on individual fitness have made the analysis of multilevel selection and its evolutionary consequences tractable and precise. The philosophical debate over the existence of multilevel selection has been statistically resolved (Wade 1978, Craig 1982, Goodnight et al. 1992, Moore et al. 1997, Agrawal et al. 2001).

We suggest that community-level selection is widespread, and that multilevel selection can be detected using contextual analysis, a conventional, statistical framework based on multiple regression (Sokal and Rohlf 1995). Contextual analysis makes use of the standard evolutionary genetic definition of selection as the covariance between phenotype, z , and relative fitness, w (Cov[w , z]; Lande and Arnold 1983, Lynch and Walsh 1998). Here, relative fitness, w , equals an individual's absolute fitness divided by the average fitness of all individuals. With contextual analysis, w is partitioned into within- and among-group components. Thus, it identifies individual and group effects on individual relative fitness (Goodnight et al. 1992). It also shows that even when selection acts *only* on individuals (e.g., soft selection; Wade [1985]), indirect effects on fitness arising from group membership contribute significantly to the total variance in relative fitness, i.e., to total selection (Crow 1958). Although this approach is limited in its ability to identify the source of genetic interactions (Agrawal et al. 2001), it does show when and how strongly multilevel selection acts. Moreover, its use removes the need to consider only situations in which the intensity of community-level selection *exceeds* that of individual selection, or those situations in which *direct* competition among communities occurs (the conditions of Johnson and Boerlijst 2002).

We can rewrite the standard equation of Goodnight et al. (1992) to include a term that accounts for community effects on individual relative fitness, w , as

$$w = b_{wz:zij:zi..}z_{ijk} + b_{wzj:z:zi..}z_{ij} + b_{wzli:z:zi..}z_{li}$$

Here, the effects of selection acting at individual, group, and community levels are identified by the three terms on the right side of the equation. Each term has two parts, a partial regression coefficient and an individual, or average, phenotype. In the first term, $b_{wz:zij:zi..}$ describes the partial regression of relative fitness on individual phenotype, with the effects of the average group and community phenotypes held constant. It is multiplied by z_{ijk} , the phenotype of the k th individual in the j th group, within the i th community. Thus, the first term measures the intensity of individual selection acting on individual phenotypes.

In the second term, the coefficient $b_{wzj:z:zi..}$ describes the partial regression of relative fitness on group phenotype, with the effects of individual and average community phenotype held constant. It is multiplied by z_{ij} , the average phenotype in the j th group. The subscript “.” represents the average across all individuals within each group. Thus, the second term measures the intensity of selection on individual phenotypes as a result of their membership within particular groups. The third coefficient, $b_{wzli:z:zi..}$ describes the partial regression of relative fitness on community phenotype, with the effects of individual and average group phenotype held constant. It is multiplied by z_{li} , the average phenotype within the i th community. Thus, the third term mea-

sures the intensity of selection on individual phenotypes as a result of their membership within particular communities.

How can these parameters be used to detect multilevel selection in nature? As an example, consider the gall-forming aphid, *Pemphigus betae*, and its cottonwood host trees. Here, aphid survival depends upon at least three factors: the genotype of the aphid (individual effects); the genotype of the tree, which influences local aphid density (group effects); and the genotypes and numbers of other organisms associated with the tree and its aphids (community effects). Aphid genotype influences its ability to form a gall and reproduce, and tree susceptibility affects the distribution and density of aphids, which in turn affect many other species. These species (e.g., arthropod and avian predators) affect aphids and the host tree. Considering the genotype of the aphid (k), the genotype of the tree (j), and the aggregate genotypes of the community of other organisms associated with each tree (i) as independent variables in multiple regression, we can quantify how each level of selection contributes to the relationship between the aphid's ability to form a functional gall (i.e., the phenotype, z) and its subsequent fecundity relative to other aphids (i.e., relative fitness, w).

To understand community evolution, we must understand four phenomena: (1) the nature of genetic variation underlying traits within species; (2) how trait interactions within and among species contribute to the among-community component of phenotypic variance (e.g., community heritability); (3) how these direct and indirect genetic effects influence the relative fitness of individuals and communities; and (4) how selection acts at hierarchical levels within communities. Identifying the levels at which selection is most powerful will reveal whether individual-, group-, and community-level selection have significant effects on relative fitness. This will allow researchers to focus their efforts on the *causes* of fitness differences. Once traits that represent the extended phenotypes of dominant and keystone species are identified, their influence on other species can be rigorously explored with factorial exclusion experiments. Controlled crosses, QTL, and sequence analyses can then be used to explore the genetic architectures underlying these traits.

Four major points are raised in this section. (1) The issue of group selection vs. individual selection is outmoded; selection can operate simultaneously at multiple levels. (2) Due to the heritability of extended phenotypes and multiple levels of selection, community evolution is likely. (3) Realistic statistical methods and experiments allow us to measure the relative importance of selection acting at different levels. (4) To the extent that species interactions affect genetic covariances, species evolution must be placed in a community context.

CONCLUSIONS

Throughout our development of community genetics, at every level of examination, our perspective reveals the consequences of an extended phenotype. The extended phenotype can be traced from the individuals possessing the trait, to other trophic levels, to the community, and to ecosystem processes such as N mineralization (e.g., Fig. 3). The effects of these extended phenotypes on ecosystem processes can be exerted in remarkably few steps and need not be diffuse. Our studies suggest that these extended phenotypes are most likely to have community and ecosystem consequences when expressed in dominant or keystone species. Because most communities have both, and they often interact (e.g., Fig. 2), we expect the effects of their combined extended phenotypes to be extensive. Conserving genetic variation in dominant and keystone species may be especially important due to the dependence of other species on a subset of the genome of these community drivers (i.e., the concept of the minimum viable interacting population, MVIP). Because environment influences gene expression ($G \times E$), extended phenotypes that are not expressed in one environment can be expressed as environments change, cascading to affect multiple trophic levels with unexpected and large consequences. For this reason, the effects of global change and human impacts on the extended phenotypes of dominant and keystone species are especially important to understand.

The experimental demonstration that community composition and species richness can be heritable (e.g., Fig. 1) is an important step toward understanding community structure and evolution in the wild. In combination, extended phenotypes and community heritability enhance the likelihood of community evolution. Regardless of one's position on this controversial issue, tractable experiments and analyses exist to critically test these hypotheses. Because species interactions structure and define communities and ecosystems, the development of a community genetics perspective should help us to understand the natural world, its complex interactions, and the effects of anthropogenic change.

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