
Note: The editor would not provide final copy, so these galleys contain a few minor errors. For example, substitute $H'$ in the legend of Fig. 3 and the page numbers are incorrect as a box was inserted into the text, which doesn’t show in these galleys.
3 A community and ecosystem genetics approach to conservation biology and management


INTRODUCTION

The emerging field of community and ecosystem genetics has so far focused on how the genetic variation in one species can influence the composition of associated communities and ecosystem processes such as decomposition (see definitions in Table 3–1; reviews by Whitham et al. 2003, 2006; Johnson & Stinchcombe 2007; Hughes et al. 2008). A key component of this approach has been an emphasis on understanding how the genetics of foundation plant species influence a much larger community. It is reasoned that because foundation species structure their ecosystems by creating locally stable conditions and provide specific resources for diverse organisms (Dayton 1972; Ellison et al. 2005), the genetics of these species as “community drivers” are most important to understand and most likely to have cascading ecological and evolutionary effects throughout an ecosystem (Whitham et al. 2006). For example, when a foundation species’ genotype influences the relative fitness of other species it constitutes an indirect genetic interaction (Shuster et al. 2006), and when these interactions change species composition and abundance among individual tree genotypes, they result in individual genotypes having distinct community and ecosystem phenotypes. Thus, in addition to an individual genotype having the “traditional” phenotype that population geneticists typically consider as the expression of a trait at the individual and population level, community geneticists must also consider higher-level phenotypes at the community and ecosystem level. The predictability of phenotypes at levels higher than the population can be quantified as community heritability (i.e., the tendency for related individuals to support similar communities of organisms and ecosystem processes; Whitham et al. 2003, 2006; Shuster et al. 2006).

Numerous studies in diverse systems demonstrate that community and ecosystem phenotypes exist (e.g., cottonwoods – Dickson & Whitham 1996; Whitham...
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Table 3-1. Definitions of community genetics terms

<table>
<thead>
<tr>
<th>Term</th>
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<tr>
<td>Community and ecosystem genetics</td>
<td>The study of the genetic interactions that occur among species and their abiotic environment in complex communities</td>
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<tr>
<td>Community and ecosystem phenotypes</td>
<td>The effects of genes at levels higher than the population. These phenotypes result from interspecific indirect genetic effects, which can be summarized as a univariate trait.</td>
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<tr>
<td>Community heritability</td>
<td>The tendency for related individuals to support similar communities of organisms and ecosystem processes</td>
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<tr>
<td>Foundation species</td>
<td>Species that structure a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes</td>
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<tr>
<td>Minimum viable population (MVP)</td>
<td>The size of a population that, with a given probability, will ensure the existence of the population for a stated period of time</td>
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<tr>
<td>Minimum viable interacting population (MVIP)</td>
<td>The size of a population that is required to maintain genetic diversity at levels required by other dependent and interacting species in a community context</td>
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Having demonstrated that different plant genotypes support different communities, new emphasis must be placed on understanding the implications of these findings. For example, relatively few studies have quantified how the genetic variation in foundation species might also affect the evolution of dependent community members (e.g., review by Mopper 1996 and more recent studies on oaks – Mopper et al. 2000; goldenrod – Craig et al. 2007; cottonwood – Evans et al. 2008), how the genetic variation in a foundation species in one community might affect another community (e.g., terrestrial affects aquatic – Driebe & Whitham 2000; LeRoy et al. 2006, 2007; Lecerf & Chauvet 2008), and how a community might feed back to affect the survival and performance of the genotype expressing the trait (e.g., soil microbial community impacts on a host tree; Fischer et al. 2006; Schweitzer et al. 2008). These frontiers of research remain important for a community genetics approach to reach its full conceptual potential. Based on our current knowledge, however, it seems clear that this approach can offer productive insights into conservation biology and management. The remainder of this chapter considers the conservation implications of the existence of heritable community and ecosystem phenotypes.
Whitham, Gehring, Evans, LeRoy, et al.

CONSERVATION IN A COMMUNITY CONTEXT

There are two main reasons to support a community genetics approach for conservation and management. First, because all species have evolved in a community context of many interacting species and their abiotic environments, it is unrealistic to study any one species in isolation as if it had evolved in a vacuum (e.g., Thompson 2005; Wade 2007). Thus, the community context of species evolution is far more realistic as it considers more of the variables that are likely to have influenced the evolution of any one species.

Second, and perhaps more important from a manager’s perspective, a community approach is less likely to result in management errors. For example, as a two-way interaction, mistletoes are clearly parasites of flowering plants. Few interactions are just two-way interactions, however. In their studies of one-seed juniper (*Juniperus monosperma*) and its associated mistletoe (*Phoradendron juniperinum*), van Ommeren and Whitham (2002) found that the berries produced by both the juniper and the mistletoe were primarily dispersed by birds such as Townsend’s Solitaires (*Myadestes townsendi*). If the seeds of mistletoe attract more birds that end up dispersing more juniper berries, then as a three-way interaction, mistletoe might be considered as a mutualist rather than a parasite. In support of this hypothesis, they found that juniper stands with mistletoe attracted up to 3 times more birds than did stands with little or no mistletoe. Most importantly, the number of juniper seedlings was more than twofold greater in stands with high mistletoe density compared with stands that had little or no mistletoe. A manager would be justified in the case of a two-way interaction in removing mistletoe to promote tree performance. In the case of a three-way interaction, however, the opposite strategy might be warranted because the mistletoe benefits juniper recruitment by promoting avian seed dispersal. Thus, just by adding one additional species to the analysis, the fundamental relationships of juniper and mistletoe can “switch or reverse” from negative to positive, and management decisions would also shift accordingly. Because the species composing a community interact, the sign of the ecological interaction and the appropriate management decision is dependent on the number of interacting players and their combined interactions.

Although the previously mentioned study demonstrates how a community analysis versus a population analysis can result in a qualitative change in interpretation that affects management decisions, it is important to know whether such reversals in interpretation are common enough to warrant concern. Bailey and Whitham (2007) reviewed 85 studies and 417 tests that varied in the number of factors examined in scientific studies, which included numbers of species, geographic scale (e.g., local to global), and number of years of the study (Fig. 3–1). When the study included only one factor, there was no chance of detecting either a significant interaction or a reversal in outcome as it is beyond the ability of the statistical approach. When two factors were included in the study, however, there was a 55% probability of detecting a significant interaction term (solid bars), and this probability increased to nearly 95% when four factors were included in the analysis. Note that such an interaction term could be just a “quantitative” change in which the sign of an interaction would still remain
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Figure 3–1: A survey of the literature shows that interaction effects and pattern reversals are common, which argues for a community approach to avoid potentially costly errors in conservation and management decisions. Solid bars show that as the number of factors in a study increases, the observed percentage of significant interaction effects also increases (i.e., both quantitative and qualitative interactions). Open bars show that, as the number of factors in a study increases, the observed percentage of reversals also increases (i.e., a qualitative change in the sign of an interaction). Figure from Bailey and Whitham (2007).

the same (i.e., negative remains negative, and positive remains positive). More importantly, they found that, as the number of factors increased, the number of reversals also increased such that, when the analysis included four factors, there was a nearly 80% probability that the sign of the interaction of one or more factors reversed from negative to positive or from positive to negative. These “qualitative” changes in interpretation are the most vexing, as they have a high probability of resulting in fundamental management errors. This study concluded that, to avoid such errors, conservation biologists and managers need to adopt a long-term, community approach that covers a large geographic area.

Because species interact with one another (i.e., it is a multivariate world), only by including the major interacting species can one really understand the sign of the interactions. This is why a community approach is desirable and is less likely to result in management errors that are both costly and produce unintended effects.

HERITABLE COMMUNITY AND ECOSYSTEM PHENOTYPES

To justify a community genetics approach it is essential to demonstrate that community and ecosystem phenotypes exist and that they are heritable. Although
Community and ecosystem phenotypes of individual tree genotypes of *P. angustifolia* show broad-sense heritability ($H^2$). Significant heritability of the canopy arthropod community, soil microbial community, trophic interactions between birds and insects, and soil nutrient pools demonstrate how trait variation in a foundation tree can structure communities and ecosystem processes ($H^2_C$ for community traits; $H^2$ for single ecosystem trait). Because soil microorganisms mediate many ecosystem processes, including litter decomposition and rates of nutrient mineralization, the formation of these communities may feed back to affect plant fitness. Solid lines indicate known interactions; dashed lines indicate possible interactions. Quantitative genetic patterns such as these argue that genomic approaches will enhance our understanding of how interacting community members influence ecosystem processes. Figure from Whitham and coworkers (2008).

Figure 3–2: Community and ecosystem phenotypes of individual tree genotypes of *P. angustifolia* show broad-sense heritability ($H^2$). Significant heritability of the canopy arthropod community, soil microbial community, trophic interactions between birds and insects, and soil nutrient pools demonstrate how trait variation in a foundation tree can structure communities and ecosystem processes ($H^2_C$ for community traits; $H^2$ for single ecosystem trait). Because soil microorganisms mediate many ecosystem processes, including litter decomposition and rates of nutrient mineralization, the formation of these communities may feed back to affect plant fitness. Solid lines indicate known interactions; dashed lines indicate possible interactions. Quantitative genetic patterns such as these argue that genomic approaches will enhance our understanding of how interacting community members influence ecosystem processes. Figure from Whitham and coworkers (2008).

Numerous studies in diverse systems have shown that different genotypes support different community members and ecosystem processes (see references in the introduction), only a few studies have quantified the heritability of community and ecosystem phenotypes (e.g., arthropod diversity on evening primrose – Johnson & Agrawal 2005; Johnson et al. 2006; arthropod community composition, soil microbial community composition, and trophic interactions on narrowleaf cottonwood – Bailey et al. 2006; Shuster et al. 2006; Schweitzer et al. 2008; respectively). For example, Fig. 3–2 shows that the canopy arthropod community on narrowleaf cottonwood (*Populus angustifolia*) was under strong genetic control such that, regardless of where replicate clones of the same tree genotype were planted within a common garden, they tended to accumulate and support the same community of arthropods (Shuster et al. 2006). Because Shuster and coworkers used replicate clones of individual tree genotypes, they calculated...
broad-sense community heritability ($H^2_c$), which estimates that genetic factors account for approximately 60% of the variation in the canopy arthropod community ($H^2_c = 0.60$).

In another common garden study of the soil microbial community, Schweitzer et al. (2008) assessed the microbial community composition in bulk soil beneath tree canopies by using phospholipid fatty acid (PLFA) biomarkers (Fig. 3–2). PLFAs are unique to major taxonomic groups (e.g., Gram-positive and -negative bacteria, and fungi), and thirty different groups were identified. Their analysis found a strong tree genetic component to microbial community composition ($H^2_c = 0.70$). Schweitzer et al. (2008) also found that soil microbial biomass nitrogen exhibited high broad-sense heritability ($H^2 = 0.61$), indicating a genetic basis for soil nitrogen pools stored in microorganisms. This latter finding is important because soil microorganisms mediate many ecosystem processes, including litter decomposition, rates of nutrient mineralization, and nutrient pools. Because these nutrient pools are genotype dependent, the formation of different microbial communities beneath different tree genotypes may feed back to affect plant fitness. If so, such feedbacks would establish a crucial link between the microbial community and plant fitness that could pave the way for ecosystem science to be placed within an evolutionary framework (Bever et al. 1997; Hooper et al. 2000; Whitham et al. 2003; Bartelt-Ryser et al. 2005).

The potential for similar feedbacks on plant performance also exists aboveground in the interactions of insect herbivores and their avian predators (Fig. 3–2). For example, the presence or absence of the leaf-galling aphid (Pemphigus beta) is determined by susceptible or resistant tree genotypes. This interaction predictably affects other trophic levels and alters the composition of a diverse community of fungi, insects, spiders, and avian predators (Dickson & Whitham 1996; Bailey et al. 2006). In combination, these and other studies described previously suggest that indirect genetic interactions among relatively few foundation species (e.g., tree, herbivore, predator, mutualist, and/or pathogen) and their environment may structure the composition and abundance of a much larger community of organisms, which could then feed back to affect the performance of individual tree genotypes.

An important goal for understanding the ecology, evolution, conservation, and management of any ecosystem is to define how many foundation species (plants, animals, microbes) define a given ecosystem and their extended effects on associated species. Understanding the genetics (genotypic or genetic variation therein) of foundation species in a community context is likely to be more informative than the genetics of most other species (e.g., rare species) and should result in fewer management errors than would single-factor or -population approaches. So far, our findings suggest that the study of relatively few foundation species in a community context can tell us much about a larger system involving many species. If correct, then the conservation and management of whole ecosystems may be more tractable than previously thought as all species are not equally important in “driving” the system. Focusing on foundation species does not imply that other organisms such as rare species are not important or deserving of preservation. It simply argues that the interactions of relatively few species structure an ecosystem and that many species respond to rather than create
the conditions required by other species for their survival. If concentrating on
the community genetics of foundation species proves generally correct, it would
greatly simplify the dilemma of having to understand the complex interactions
of all species to make appropriate management decisions, which is a daunting if
not impossible task.

CONSERVATION CONSEQUENCES OF HERITABLE PHENOTYPES

If different genotypes of a foundation tree species support different community
members and ecosystem processes as the previously mentioned heritability stud-
ies demonstrate, several key predictions can be made, which are of conservation
and management value.

First, if different tree genotypes support different communities, we would
expect that the genotypes that are genetically most similar will support the
most similar communities. At both local and regional levels, Bangert and col-
leagues (2006a,b) found that genetically similar cottonwoods supported similar
arthropod communities, whereas genetically dissimilar plants supported more
different communities (i.e., a genetic similarity rule hypothesis). For example,
by using a Mantel test to compare the molecular marker and arthropod community
matrices of individual trees, we found that trees that were the most genetically
similar were also the most similar in their arthropod communities (Fig. 3–3).
This pattern holds for trees growing in a common garden, for trees growing in
the wild in a single river (Fig. 3–3; Bangert et al. 2006a), and for trees growing
throughout the American West in multiple river systems covering 720,000 km²
(Bangert et al. 2006b). Studies with the forest tree (Eucalyptus globulus) in Aus-
tralia showed a similar pattern in which the most genetically similar trees and
geographic races also supported more similar canopy communities (Barbour et
al. 2009). In both studies the correlation in divergence in molecular and commu-
nity variation was mediated through correlated divergence in quantitative traits
such as leaf morphology and chemistry. Although it is well known that many
specialist insects may show corresponding divergence that is correlated with the
divergence of their host plant species (e.g., Abbot & Withgott 2004), it appears
that the same pattern holds for less specialized community members. From a
conservation perspective, the findings of Figs. 3–2 and 3–3 argue that genetic
diversity in a foundation tree species matters for the dependent community of
microbes, arthropods, and vertebrates.

Second, if different tree genotypes support different communities, then greater
 genetic diversity in a foundation species should be directly correlated with greater
community diversity. Based on this prediction, Wimp and colleagues (2004) used
amplified fragment length polymorphism (AFLP) molecular markers to quan-
tify genetic diversity in eleven different stands of cottonwoods growing in a
hybrid zone along the Weber River in Utah. The arthropod community was then
recorded for the same trees, and the researchers found that stand genetic diversity
accounted for approximately 60% of the variation in the diversity of an arthropod
community composed of 207 species (Fig. 3–4). Similar findings were obtained
with oaks (Quercus spp.; Tovar-Sanchez & Oyama 2006). Experimental studies
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Figure 3–3: Because genetically similar trees support similar communities of organisms, (i.e., the Genetic Similarity Rule), genetic diversity in a foundation plant species is likely to support greater biodiversity in the associated community. On average, Mantel tests show that arthropod communities become less similar as plant genetic distance increases (i.e., small genetic distance indicates more closely related trees). Genetic distances of the common garden trees (solid circles) were based on restriction fragment length polymorphism (RFLP) markers. The genetic distances of the naturally growing trees in the wild (open triangles) were based on AFLP marker data and include only the F1 and backcross hybrids, thus removing the leverage of the two pure parental species from the analysis. Figure from Bangert and colleagues (2006a).

that manipulated genetic diversity with evening primrose (*Oenothera biennis*) and goldenrod (*Solidago altissima*) also showed that genetically diverse patches supported significantly greater species richness than did monocultures (Crutsinger et al. 2006; Johnson et al. 2006; respectively).

Third, if individual plant genotypes support different communities, they also may drive genetic differentiation and speciation in dependent community members. Several studies have found that populations of herbivores are adapted to individual host genotypes (Karban 1989; Mopper et al. 1995, 2000; Mopper 1996; Evans et al. 2008). Because speciation may follow from locally adapted, differentiated populations of arthropods (Via 2001; Dres & Mallet 2002), conserving genotypic diversity in foundation species can conserve locally adapted populations of arthropods. Conserving genotypic diversity in foundation species to conserve locally adapted populations of dependent species may extend to multiple trophic levels. For example, multiple herbivores (Stireman et al. 2005) and their parasitoids (Stireman et al. 2006) are genetically differentiated on two closely related sympatric species of *Solidago* indicating that host plants can affect species' evolution at multiple trophic levels. A major conclusion from such studies is that genetic diversity is far more than just an endangered species issue; it is also important for common foundation species in which different plant genotypes support different community members.
Fourth, when different genotypes of a foundation species support different communities, management practices based on species-area relationships may need to shift to genetic diversity-area relationships. In other words, is the species-area curve really driven by area, is it driven by the genetic diversity of the foundation species, or is it driven by both? To answer this question, Bangert et al. (2008) quantified the arthropod species accumulation curve for broadleaf cottonwoods (Fig. 3–5A). This curve shows that, as the arthropod communities of more trees are sampled (i.e., area), arthropod species richness increases predictably and begins to plateau. This pattern is common and is a primary justification for the conservation practice of preserving large areas to capture the species pool. When molecular marker diversity for the same trees was analyzed to produce a molecular marker richness accumulation curve, the same pattern emerged. This curve shows that as the molecular markers of more trees are sampled (i.e., area), marker richness also increases predictably and begins to plateau. The two curves are remarkably similar. Furthermore, arthropod species richness is highly correlated with molecular marker richness ($r^2 = 0.92; \text{Fig. 3–5B}$). This strong correlation raises an issue: Is the species-area curve driving biodiversity, is it the genetic diversity of the foundation species that drives biodiversity, or is there some combination of the two? Although area and genetic diversity of foundation species are undoubtedly autocorrelated, from a manager’s perspective it is important to know whether a landscape should be managed from an area perspective or from
Figure 3–5: The species-area curve is also a species-genetic diversity curve, which may affect management decisions to preserve communities based on area, genetic diversity of foundation species, or both. (A) Scaling in which both arthropods and molecular markers scale similarly as a function of the number of broadleaf cottonwoods sampled (sample size or number is also a proxy for area). At their asymptotes, adequate sampling captures most of the arthropod community and genetic diversity, respectively. (B) Consistent with the above similarity in scaling, there is a strong positive relationship between arthropod species richness and marker richness. Because trees were selected at random, no geographic structure is reflected in these patterns. Figure from Bangert and colleagues (2008).

the genetic diversity of a foundation species’ perspective. Furthermore, if future conservation efforts try to establish living repositories for individual species, it is important to define the genetic diversity of these repositories that will be required to support their dependent communities.

A COMMUNITY GENETICS PERSPECTIVE ON MINIMUM VIABLE POPULATIONS

Historically, an important concept in conservation biology is the minimum viable population (MVP), which is the size of a population that, with a given probability, will ensure the existence of the population for a stated period of time (Shaffer 1981; Gilpin 1987). This concept is especially important for rare and endangered species whose populations are often small, highly inbred, and lacking in genetic diversity. Although this concept attempts to understand what population sizes are required to save a single species, it falls short of understanding what is necessary to save dependent community members and especially species that require a single host species or a subset of the host’s genotypes for their survival.

An example of how the distribution, population growth rate, and evolution of one species can be dependent on genotypic differences of another species is that of the gall-forming mite (*Aceria parapopuli*) on cottonwoods. McIntyre and Whitham (2003) found that 99% of the mite’s population was concentrated on naturally occurring F1 hybrids between narrowleaf and Fremont cottonwood (*P. angustifolia*, *P. fremontii*, respectively). Because suitable F1 hybrid hosts are rare in the wild, the “actual” host population for these mites is a small subset of the larger
cottonwood population. Furthermore, Evans et al. (2008) showed that the mites are even further differentiated such that the mites on the hybrids and parental hosts are different cryptic species. Transfer experiments showed that, even among F$_1$ hybrids, the mites can be adapted to individual tree genotypes. Thus, even though cottonwoods are common trees in riparian forests, a dependent species can still be limited by the number of suitable host genotypes.

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 host specific (Scriber 1986). Other examples are provided by Feder and colleagues (1988), Wood and Keese (1990), Roinen and coworkers (1993), and Thompson (1994). Microorganisms 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). Specificity in gene-for-gene interactions in molecular control points between plants and microorganisms in the rhizosphere is thought to be widespread in many foundation species (Hirsch et al. 2003; Phillips et al. 2003).

Such specificity suggests that MVP sizes (Shaffer 1981) in one species may be too small to support important interactions with other species (see Thompson 1994 as well as Chapter 10 by Waples and colleagues). Other researchers have recognized the weaknesses associated with the conservation of individual species rather than communities or ecosystems (e.g., Rohlf 1991; Simberloff 1998; Lindenmayer et al. 2007). A community genetics approach enhances our understanding of why the genetics of foundation species are so important, provides genetically based mechanisms to support these criticisms, and has the potential to merge different points of view as it spans genes to ecosystems.

Because of these issues, Whitham and colleagues (2003) proposed the minimum viable interacting population (MVIP) size that represents the size of a population needed to maintain genetic diversity at levels required by other dependent and interacting species in a community context. For example, MVP sizes for conserving a foundation tree species are probably much smaller than the population size required to conserve other dependent community members that require a subset of the tree’s genotypes for their survival (MVIP). Thus, MVP represents the lower end of the population size that is required to conserve the foundation species, and MVIP represents the upper end of the population size of the foundation species that is required to conserve the dependent community and their interactions. Fig. 3–6 provides an initial guide as to where the differences between MVP for a foundation species and MVIP for a foundation species and its dependent community would be expected to be highest and lowest. High community and ecosystem heritability ($H^2_c$) suggests that many community members and the ecosystem processes they drive are dependent on the individual genotypes of a foundation species, whereas a low or nonsignificant $H^2_c$ suggests that the distributions of most community members are not genotype dependent. Thus, as community heritability increases for any given foundation species, we would expect that the difference between MVP and MVIP would also increase.
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![Diagram of MVIP - Minimum Viable Interacting Population]

Figure 3–6: Illustration of the hypothesized relationship between high community heritability (i.e., different genotypes of a foundation species support different communities of organisms and ecosystem processes) and the population size needed to preserve the dependent community. As community heritability increases, the population size of the foundation species must increase to support its dependent community and the ecosystem processes they promote. The minimum viable interacting population (MVIP), takes into account the genetics-based interactions among species in a community context. See text for contrast of MVP and MVIP.

MVP and MVIP represent end points on the population-to-community continuum. They provide a conceptual mechanism to explain why conservation efforts may flounder if they do not consider the consequences of genetic variation in foundation species on the dependent community (see Chapter 9 by Leberg and colleagues). Numerous studies show that temperate and boreal trees exhibit moderate to strong clines in ecologically important traits suggesting that populations are genetically differentiated and locally adapted (Aitken et al. 2008). Associated with this genetic structuring, common garden studies by Barbour et al. (2009) showed that different geographic races of the same eucalypt species supported different communities. Although current conservation strategies target rare species, it may be even more important to conserve the genetic variation in foundation species with broad distributions, because individual genotypes and races have different community and ecosystem phenotypes.

COMMUNITY PHENOTYPES OF GENETICALLY ENGINEERED ORGANISMS

Although the incorporation of novel genes into an organism through recombinant deoxyribonucleic acid (DNA) technology has enormous potential benefits, including increasing crop yields and reducing reliance on chemical pesticides (Avise 2003), the genes introduced into genetically engineered organisms (GEOs) may have unintended community and ecosystem phenotypes that are important to evaluate. Several issues need to be considered. First, GEOs now have been introduced over large areas in both industrialized and developing economies.
For example, the global area planted with transgenic crops exceeded 110 million hectares in 2007, a 12% increase over the previous year (Lawrence 2008). Because many of these crops are grown as monocultures with little genetic variation, they are, in effect, both a foundation species and a foundation genotype.

Second, there is increasing evidence that transgenic organisms can move beyond their intended destinations where they have the potential to persist and to hybridize with native species (see Chapter 2 by Schaal and colleagues). Maximal gene-flow distances of 21 km were observed in herbicide (glyphosate)-resistant creeping bent grass (*Agrostis stolonifera* L.), a wind-pollinated, out-crossing, perennial turf grass planted in test fields in Oregon (Watrud et al. 2004). Three years after the test fields were taken out of production, 62% of plants tested were glyphosate resistant (Zapiola et al. 2008). There is evidence that transgenic canola (*Brassica napus*) and sunflower (*Helianthus annuus*) hybridize with wild relatives, although the fitness of these hybrids is highly variable and frequently not greater than wild genotypes (reviewed in Chapman & Burke 2006). Recent research also suggests that the risk of environmental impact from horizontal gene transfer of bacterial genes from crops to surrounding soil microorganisms is much higher than initially supposed (Heinemann & Traavik 2004). In their review, Marvier and Van Acker (2005) concluded that movement of transgenes beyond their intended destinations is a “virtual certainty.”

A third reason that transgenics may have unintended ecological consequences for communities and ecosystems is that transgenes are designed to have significant fitness consequences (e.g., reducing herbivory, disease, or competition) thereby increasing the likelihood that transgenics will interact significantly with members of the communities in which they are introduced. Furthermore, crops with stacked traits (two or more transgenes) are now more widely planted than those containing only insect-resistance traits (Lawrence 2008).

Transgenic plants have been shown to have nontarget community and ecosystem phenotypes. For example, Bt corn byproducts can enter headwater streams where they are stored, consumed, and transported downstream to other bodies of water. Feeding trials in the laboratory indicate that Bt corn residues negatively affect nontarget stream insects (Rosi-Marshall et al. 2007). Recent meta-analyses, however, highlight the need for comparison of the effects of transgenes to those of traditional agricultural practices. An analysis of forty-two experiments showed that Bt cotton and corn altered the abundance of some taxa of nontarget arthropods, but the effects of the transgenes were much smaller than those of traditional pesticides (Marvier et al. 2007). Likewise, consistent effects of Bt corn, cotton, and potatoes on particular functional guilds of nontarget arthropods were not observed (Wolfenbarger et al. 2008). A recent review of Bt plant effects on the soil biota also found few significant impacts (Icoz & Stotzky 2008). Note that most studies of nontarget effects of transgenic organisms are relatively short-term and thus may ignore effects that accumulate slowly or are triggered by a change in environmental conditions.

A community genetics analysis provides a method for quantifying the community and ecosystem phenotypes of transgenes and their heritability. Importantly, in many ecological studies, the direct effects of a trait on an organism’s phenotype (e.g., increased resistance to pest attack) may be less important than the indirect
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Effects on the community phenotype (e.g., increased resistance to pest attack alters competitive interactions with other species to alter community structure). The movement of transgenes into wild populations, via hybridization and introgression, could alter interspecific interactions, potentially resulting in changes in the distribution of the wild population and its dependent community. Few studies of GEOS examine the consequences of transgenes on interactions, particularly indirect interactions, among organisms. In addition, subtle, initial changes in interactions between transgenic and wild populations may not be detected in short-term studies that are frequently limited in spatial scale as well. The community and ecosystem consequences of transgenes are also important to define because of the growing view that transgenes will escape from their intended destination and that they cannot be retracted after they have escaped (Marvier & Van Acker 2005). When released, some transgenes may have irreversible conservation implications for communities and ecosystems. These possible negative consequences of GEOS should be considered along with their potential benefits, such as promoting agricultural efficiency and reducing pesticide use.

COMMUNITY GENETICS AND CLIMATE CHANGE

Climate change is a “wild card” in conservation and restoration. Because of concerns about restoring only with locally adapted genotypes, the policies of most agencies require the use of local stock in restoration. Whereas this is a valid view in an unchanging world, in a dynamic world facing major vegetation shifts in response to climate change, the “local” environment may well shift so fast or so much that local genotypes will no longer be locally adapted (see also Aitken et al. 2008). In the American Southwest, the effects of climate change are pronounced and affect the distributions of pinyon pine (Pinus edulis), cottonwood (Populus fremontii), ponderosa pine (Pinus ponderosa), quaking aspen (Populus tremuloides), and pointleaf manzanita (Arctostaphylos pungens), which are foundation species of their respective communities from low elevation deserts to mountain forests (Breshears et al. 2005; Mueller et al. 2005; Gitlin et al. 2006). For example, climate-change models of Rehfeldt and colleagues (2006) predict that, by 2090, the climate envelopes for both pinyon pine (P. edulis) and saguaro cactus (Carnegiea gigantea) will shift out of Arizona, where they are currently foundation species that define their respective communities (Fig. 3–7). Such dramatic shifts in the distributions of these species are likely to represent both ecological and evolutionary events and major conservation challenges. If these shifts come about, Saguaro National Monument will no longer contain saguaros, and for saguaros to physically reach their new climate envelope in eastern Nevada, human-assisted migration will likely be required (McLachlan et al. 2007; Aitken et al. 2008).

One factor that can potentially alleviate such dramatic shifts in distribution is the potential for selection to favor more drought-adapted genotypes that allow species to persist in areas where they might otherwise go locally extinct. For example, Franks and colleagues (2007) found rapid evolution in flowering time of field mustard (Brassica rapa) in response to altered growing seasons over just seven years. Postdrought descendants of this annual bloomed earlier than did
predrought ancestors, advancing first flowering by as much as nine days. The intermediate flowering time of Ancestor × Descendant hybrids supports an additive genetic basis for this divergence. Even vertebrate species appear capable of rapid evolutionary responses to climate change. Over a thirty-year period, Grant and Grant (2002) observed rapid evolution in the shape and size of beaks of finches in association with climate change–driven changes in seed availability.

So, what is the community genetics connection to climate change? If climate change acts as an agent of selection to alter the frequency distribution of genotypes of foundation species, then their dependent communities will also be affected. For example, Whitham and coworkers (2003) showed that approximately 1,000 species of organisms from microbes to vertebrates were differentially associated with insect-resistant and -susceptible pinyon pine (P. edulis). Recent studies by Sthultz and colleagues (2009) showed that insect-resistant trees were 3 times more likely to die than susceptible trees were during a record drought and that the change in the distribution of resistant and susceptible phenotypes on the landscape had changed from resistance-dominated stands to near parity. Thus, even if a foundation species survives in a given habitat, the change in its genetic structure is likely to affect dependent community members whose distributions are also dependent on the genotypes of the foundation plant species (see earlier sections on heritable phenotypes and minimum viable populations).

Rehfeldt and colleagues (2006) used climate envelopes to predict the future distributions of many tree species of the western United States, including P. edulis. They concluded that P. edulis would be extirpated from Arizona within eighty
years. This prediction, however, did not include potentially drought-adapted genotypes of *P. edulis* or reflect the genetic variation among populations that might exist over its large geographic distribution. In contrast, a few other models have incorporated intraspecific genetic variation and demonstrated its potential influence on climate-change projections. For example, based on provenance trials involving 140 populations tested at 62 sites throughout most of the range of lodgepole pine (*P. contorta*), O’Neill and coworkers (2008) included into their models genetic differences in the performance of these populations. Because populations tend to be locally adapted, these models predicted that different populations would vary greatly in their responses to climate change and that many populations would be maladapted to their new local environment. This provenance trial approach also provides an experimental method for identifying which populations or genotypes might best survive predicted climate changes. Thus, for species for which such provenance trials already exist, the use of this powerful experimental approach could greatly enhance the precision of climate-change models.

From these examples, it would appear that climate change creates a conundrum for conservation biologists and managers. If our management policies require restoration with local genotypes, in a climate-change scenario are we then planting the very genotypes that are doomed to fail? Few studies with foundation species are in place to provide clear information for managers to make appropriate decisions (but see O’Neill et al. 2008). We need a national network of common gardens for foundation species in which genotypes from the whole range of a species’ distribution are planted reciprocally within their current range and their predicted new ranges. Only with such empirical information can we identify the specific genotypes and source populations that are best suited to current and predicted future local conditions.

**MANAGEMENT CONCLUSIONS**

A community and ecosystem genetics approach is based on the fundamental finding that individual genotypes or populations of foundation species have heritable community and ecosystem phenotypes (Fig. 3–2). Because this finding has emerged from diverse systems on different continents, our review explores five management implications: 1) Management practices should be based on conserving genetic diversity in foundation species. Because different genotypes support different communities (Figs. 3–2 and 3–3), greater biodiversity will be achieved by preserving the greatest genetic diversity in the foundation species (e.g., Fig. 3–4). 2) It is important for managers to determine if they should be managing for area, the genetic diversity of the foundation species, or some combination of both. This is due to the fact that the species-area curve (i.e., the current basis of the management practice of setting aside large geographical areas to capture the maximum number of species in preserves) is also highly correlated with the genetic diversity of foundation species-area curve (Fig. 3–5). 3) Management practices for conserving biodiversity should be based upon the minimum viable interacting population (MVIP), which is likely to be much larger than the minimum viable population (MVP). Because the distribution of many species can be dependent
on the genotypes of foundation species, the population size of the foundation species required to support all of its dependent community members is much larger than that needed to save the foundation species itself (Fig. 3–6). 4) We need management protocols that specifically quantify the unintended ecosystem effects of genetically engineered organisms (i.e., their community and ecosystem phenotypes) as part of the evaluation process for commercial release. 5) Managing for climate change by establishing provenance trials of foundation species throughout their current and predicted range is needed to identify the genotypes and source populations that are most likely to survive, reproduce, and support their dependent communities in a new climate. These are a few of the management issues that arise when we apply a community and ecosystem genetics approach rather than just a population genetics approach.

As an initial step to achieve these goals, it would be especially helpful and cost effective if managers tagged and mapped the donors used for propagation (both for seeds and cuttings) and then tagged the individuals used in restoration plantings. Although such “bookkeeping” would represent a small fraction of the overall cost of a restoration project, the value added could be great and result in cost savings in future restoration projects. If multiple source populations and genotypes were used, managers could identify which genotypes and source populations were best adapted to a specific planting site. Long-term data is especially important as those genotypes that perform best under current climatic conditions may not be the best with future climatic conditions (e.g., Stultz et al. 2009). Performance data combined with climate change models could be used to identify which source populations and genotypes might best suit a predicted future climate. Because many plants used in restoration are long-lived, after tagged restoration sites are established, they can also be used for the life of the site to quantify the diverse communities of organisms they support as a function of the individual genotypes and source populations used in the restoration project. Because species evolve in a community context, then we must ultimately conserve and manage species in a community context.

REFERENCES

A community and ecosystem genetics approach to conservation


A community and ecosystem genetics approach to conservation


Whitham, Gehring, Evans, LeRoy, et al.


