

SPECIAL FEATURE

Community Genetics: New Insights into Community Ecology by Integrating Population Genetics¹

Community genetics is the study of the interaction between genes within a species and populations of other species in a community. This area of research was first introduced by Janis Antonovics (1992 [Toward community genetics. Pages 426–429 in R. S. Fritz and E. L. Simms, editors. *Plant resistance to herbivores and pathogens: ecology, evolution and genetics*. University of Chicago Press, Chicago, Illinois, USA]) as a modern attempt to integrate community ecology and evolution. Research programs in community genetics span from understanding the mechanistic bases of the evolution of organisms in a community context to identifying the role of genetic variation in generating community patterns. Is community genetics an emerging subdiscipline that finally unites multispecies ecology with the genetics of evolutionary change? It is argued that a mature understanding of either ecological communities or the evolution of species will require community genetics. Others cry that this label is nothing more than funding-agency-style renaming of perfectly good, classic questions in evolutionary ecology. I have asked two of the leading groups in community genetics to lay down the definitions and set the agenda for future work: Neuhauser et al., who established a Center for Community Genetics at the University of Minnesota; and Whitham et al., who have been studying the consequences of genetic variation for diverse communities and community processes. The result is two fresh and controversial lead papers. Following these papers are commentaries from eight respondents. Some of these authors were pioneers in bridging the fields of community ecology and evolution; others are newcomers seeking to infuse ecology with novelty. The result is a mix of arguments that illustrate the vigorous debate within modern community ecology.

The feature starts and ends with perspectives articulated by Janis Antonovics. Neuhauser et al. and Whitham et al. loosely follow Antonovics's (1992) reductionist and holist perspectives, respectively. The hallmark of the reductionist approach (Neuhauser et al.) is to document rapid evolutionary change. As nonequilibrium communities are affected by anthropogenic or other influences, strong interactions catalyze flux in abundances of individuals in multispecies communities, and these changes can rapidly alter the genetics of community members. It is argued that incorporation of spatial dynamics and population biology in interacting species is necessary to predict the eventual ecological and evolutionary outcome of perturbation. On the holistic side (Whitham et al.), the goal is to understand the consequences of particular genes (or gene combinations) in a community on higher levels of biological organization. Here, the influence of particular genetic variants on communities and ecosystem properties is examined in more or less equilibrium communities. Variation generated by hybridization between species has been the primary tool used to study the role of particular genes on communities; little is currently known about the role of variation within a single species. In addition, the role of genetic variance or diversity in a population in generating higher-level community properties such as productivity and species diversity is a central goal of the holistic approach to community genetics.

Perhaps nobody could cogently argue that ecology and evolution can be disciplines without each other. Yet the respondents disagree in terms of the projected role for community genetics in ecology. Tension persists over the possibility of natural selection acting on levels higher than the individual. There is a persuasive call for examining and accounting for the influence of interspecific (phylogenetic) relatedness within community studies. Add all this to the nagging age-old questions of how to define a community, who the important dominant or keystone members are, and how to assess the relative importance of various factors influencing community structure.

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Although we may be able to agree that it is a worthy goal to integrate more than one or two species into the study of population genetic change and to integrate genetics into the study of community patterns, will the reductionist and holistic approaches ever meet? Perhaps the study of coevolution in real communities (diffuse coevolution) will be the first benefactor of the combined reductionist and holistic approaches to community genetics. Others will soon follow. Ultimately, the goal is to develop an increasing ability to describe and predict patterns in nature.

—ANURAG A. AGRAWAL,
Special Features Editor

Key words: coevolution; diversity; group selection; intraspecific variation; multilevel selection; phylogenetics of communities; population genetics; species richness.

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COMMUNITY GENETICS: EXPANDING THE SYNTHESIS OF ECOLOGY AND GENETICS

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Abstract. Community genetics synthesizes community ecology and population genetics and yields fresh insights into the interplay between evolutionary and ecological processes. A community genetics framework proves especially valuable when strong selection on traits results from or impinges on interspecific interactions, an increasingly common phenomenon as more communities are subject to direct management or anthropogenic disturbances. We draw illustrations of this perspective from our ongoing studies of three representative communities, two managed and one natural, that have recently undergone large perturbations. The studied communities are: (1) insect pests of crop plants genetically engineered to produce insecticidal toxins; (2) insect-pollinated plants in habitats severely fragmented by agriculture and urbanization; and (3) a pathogen and its crop host now grown extensively outside their native ranges. We demonstrate the value of integrating genetic and ecological processes to gain a full understanding of community dynamics, particularly in nonequilibrium systems that are subject to strong selection.

Key words: anthropogenic disturbance; Bt maize; community genetics; *Echinacea angustifolia*; evolution of resistance; genetic engineering; habitat fragmentation; nonequilibrium dynamics; plant–insect interactions; plant–pathogen interactions; *Ustilago maydis*.

INTRODUCTION

Janis Antonovics (1992) articulated a vision for a new field of inquiry, “community genetics” (a term suggested by Dr. J. P. Collins, Arizona State University), to investigate the “role of genetic variation in influencing species interactions and determining community structure.” Community genetics is a synthesis of community ecology and evolutionary genetics; it directly assesses the interplay between genetic variation and community dynamics to develop a mechanistic understanding of the evolution of organisms in the context of the communities that they occupy.

Our community concept is that developed by Gleason (1917, 1926, 1927), demonstrated by Whittaker (1956), and supported by the work of Davis (1981) on community assembly. In this concept, species assemble in communities according to their individualistic attributes. We superimpose on this concept a contemporary understanding of the ubiquity of genetic variation. Thus, a community is the multispecies assemblage of genetically variable populations that together occupy

a given place. The strength of interaction between members of a community varies. Strong interactions can arise even for species that have associated only recently. For example, in the case of species invasions, strong interactions may be apparent from the time that a species arrives at a given location (Pritchard and Schluter 2001). Assembly of novel communities may have evolutionary, as well as ecological, consequences within few generations (Reznick et al. 1997, 2001, Davis and Shaw 2001). When, in addition, ecological interactions strongly influence the genetic composition of populations, the conceptual framework of community genetics becomes valuable.

Community genetics addresses questions about the evolution of interactions among organisms in a broader context than that of the more stringent framework of coevolution where “an evolutionary change in a trait . . . in one population in response to . . . a second population, [is] followed by an evolutionary response by the second population to the change in the first” (Janzen 1980). A situation in which the ecological success of one species depends on the genotypes of a second species would not necessarily be considered coevolution by Janzen’s stringent criteria, but would fit well into the framework of community genetics, whether or not the genetic composition of populations of the first species is affected by the ecological interaction. For example, invasion of a novel pathogen could dramatically affect the population genetic structure of a

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host, without reciprocal genetic effects on the pathogen population (Alexander et al. 1996).

Community genetics focuses on feedbacks between ecological interactions within and among species and genetic variability within species. It acknowledges that these feedbacks can operate on the scale of a few generations. As conceived by Levin and Udovic (1977) for a pair of species, the community genetics approach allows for rapid evolutionary change contingent on community composition. It does not view a species as a taxonomic unit as in purely ecological studies (e.g., Tilman et al. 1997), but rather as a collection of populations for each of which the genetic composition may depend on the community context and population history. Thus, the genetic composition of populations within a species may differ substantially from one community to another. We argue that a community genetics framework is particularly valuable when (1) an abrupt change in community structure, e.g., with anthropogenic disturbances, or (2) historical process of community assembly generate nonequilibrium communities and impose strong selection on members of a community.

Community genetics emerged from ecological genetics by the inclusion of a community context. Collins (1986) traces ecological genetics back to the beginning of the 20th century; some of its roots also trace back to Fisher (1927) and Dobzhansky (1947). Collins points out that during the initial development of the field of ecology, evolutionary thinking was pervasive, quite soon, however, ecological and evolutionary studies diverged as ecological studies increasingly focused on identifying proximate causes of distributions and the abundance of organisms.

Ecological genetics emphasizes the importance of considering both ecological conditions and genetic composition in studying population and community dynamics. Early studies in ecological genetics sought to explain genetic differences among populations in relation to the biotic and abiotic environment (Dobzhansky 1941, Birch 1960, Ford 1964). Classic examples include studies of melanic forms of moths in relation to air pollution (Kettlewell 1955), of tolerance of soil contamination by heavy metals (Bradshaw 1952, Antonovics et al. 1971), of mimicry in lepidoptera (van Zandt Brower 1958), and of banding patterns of snail shells (Cain and Sheppard 1954).

Observing that ecological and evolutionary processes commonly occur on the same temporal scale and that evolutionary change is detectable in a single generation, Antonovics (1976) advanced an integrated view of evolution and ecology for studies of species abundance and diversity. Antonovics and Levin (1980) further pointed out that the spatial scale of ecological processes may be smaller or larger than that of evolutionary processes, and that both may differ from the spatial scale of selection. As a consequence, without an understanding of the underlying genetic structure of

populations and their evolutionary histories, it may be difficult to understand and impossible to predict ecological patterns, even in simplified, experimental communities. A number of coevolutionary studies using laboratory experiments, empirical studies of natural populations, and theoretical approaches have demonstrated that the outcome of genetic and ecological interplay may not be readily predictable at the outset of an experiment. For example, in experiments with *Escherichia coli* infected by the virus T5, the susceptible genotype was driven to extinction following the origin and spread of a resistant genotype. However, when susceptible *E. coli* were infected by the virus T4, a resistant host type emerged that coexisted with the susceptible host type. A cost of resistance at low viral titers might have been the mechanism for coexistence (Lenski and Levin 1985). These two experiments demonstrated that communities may evolve along different paths to different equilibria. More importantly, such experimental community approaches illustrate that when genetic parameters are included, predictive models can be developed for conditions under which alternative outcomes might be expected. Community genetics provides a framework for such studies.

Consideration of the potential for rapid evolutionary change and how this may differ among populations has been extended to the case of climate change by Etterson (2000) and Etterson and Shaw (2001) in a study of three populations of an annual legume, *Chamaecrista fasciculata*, drawn from a range of 1000 km. Treating this species' extensive latitudinal and climatic range as a proxy for the rapid warming projected over the coming decades, Etterson documented both strong selection on a Minnesota population when grown in Kansas and Oklahoma, and considerable genetic variation in traits under selection. However, this study also demonstrated that antagonistic genetic correlations between traits are likely to impede evolutionary response, causing it to lag behind the predicted change in climate.

Thompson's (1994, 1997) concept of a geographic selection mosaic further frees the study of evolutionary interactions from the constraints of strict coevolutionary definitions (Janzen 1980). By focusing on ecological interactions of organisms in metapopulations, the geographic selection mosaic accounts for spatial variation of selection across different communities. Interactions between organisms vary qualitatively across a species' range, such that in some communities, strong interactions occur (hot spots), whereas with a different community composition, the same organisms affect each other's fitness only weakly (cold spots). Spatial differences in selection due to intraspecific genetic variation can both affect and be affected by the community composition.

An attractive feature of the geographic mosaic hypothesis is that it yields the following testable predictions (Thompson 1999). (1) Traits may vary among populations; in particular, they will be similar in some

communities but not in others. (2) There is potential for different outcomes of interspecific interactions due to genetic differences among populations and to differences in the abiotic or biotic environment. (3) Where the range of a species extends over a mosaic community such that interactions and, consequently, selection vary, coevolved traits may not occur throughout the range. Long-term studies, such as the *Silene-Myco-botrium* system (Antonovics 1992, Alexander et al. 1996), the *Greya-Lithophragma* system (Thompson 1999), and the *Linum-Melampsora* system (Burdon and Thrall 1999) provide evidence for the geographic selection mosaic.

THE CONCEPTUAL FRAMEWORK

The community genetics framework promotes new understanding when selection alters genetic composition on the same time scale as that on which numerical abundances change. Such concordant change is expected, with strong selection acting on traits mediating interspecific interactions. In these cases, ecological and evolutionary processes can no longer be treated separately. Although evolutionary genetics addresses strong selection and the potential for rapid evolution (Dobzhansky 1941), for instance, insecticide resistance (Georghiou 1986, Lenormand et al. 1999, Raymond et al. 2001), drug resistance (Garrett 1994), and the evolution of competitors (Pimentel and Al-Hafidh 1965, Pimentel et al. 1965), the potential for evolutionary change over a few generations remains underappreciated. Darwin (1859), despite acknowledging rapid evolution in artificial selection, regarded natural selection as a weak force apparent only over the geological time scale. Moreover, analysis of the consequences of strong selection poses significant theoretical challenges; although these have not been insurmountable (e.g., for quantitative genetics, Turelli and Barton [1994]), theoretical work has concentrated more heavily on the more tractable case of weak selection (e.g., Kimura 1964, Kingman 1982, Neuhauser 1999). Thus, the frequently mentioned distinction between evolutionary and ecological time scales is reflected in a modeling framework in which theoretical analyses assume weak selection on the order of the inverse of the population size, and imply that the effects of selection must be manifested on a time scale on the order of the population size. In many population genetic models (e.g., Kimura 1985), noticeable changes take thousands to millions of generations when the system is not in equilibrium. In contrast, in standard ecological models such as logistic growth or Lotka-Volterra competition models, noticeable changes occur from one generation to the next when the system is not in equilibrium. Treated in this way, weak selection has only subtle effects on population genetic dynamics over a few generations, whereas ecological changes may be considerable, thus resulting in a separation of time scales.

Both theoretical and empirical studies that simultaneously address ecological and evolutionary factors face challenges. Theoretical studies face the challenge of multidimensionality. Even in the simplest framework of ordinary differential equations, two equations are needed to model the ecological interactions of two species. Adding genetic variation to one or both species quickly increases the number of equations beyond that which is analytically tractable. However, multidimensional models permit complex behavior (multiple stable equilibria, limit cycles, and chaos) and explicit consideration of spatial dynamics, such as in Thompson's (1999) geographic selection mosaic. Empirical studies can be similarly challenged by multidimensionality. Experiments to assess effects of multiple factors and their interactions require many treatment combinations and, with replications, become very large. If the outcome of interactions varies in space and time, only long-term studies over large spatial scales reveal the full range of realized outcomes. Moreover, with variation over space and time, comparison among data sets is compromised and outcomes may appear unpredictable. Multidimensionality can also result in a proliferation of model parameters that cannot be adequately estimated in empirical studies.

We are optimistic that an integrated approach will ultimately result in a general framework that can accommodate the complexities that arise from considering ecological and evolutionary processes simultaneously. We argue that the value of an integrated, community genetics approach is particularly great under three conditions: nonequilibrium, genetic variation within species, and strong selection. We claim that the co-occurrence of these three conditions is not rare.

We present empirical studies together with mathematical models for which the framework of community genetics is particularly useful. These studies are characterized by strong selection following a large perturbation. The theoretical models are informed by empirical studies and include both ecological and evolutionary dynamics; leaving out one or the other aspect weakens the model predictions.

The first two studies investigate the interplay of ecological and evolutionary dynamics in the evolution of resistance to transgenic crops (*Bt* maize). Evolution of resistance is often modeled neglecting much of the ecological context. We demonstrate that adding ecological interactions (such as population regulation or density-dependent predation rates) can alter the predictions of simpler evolutionary models. The large-scale introduction of a transgenic crop, which represents a selection episode at an unprecedented scale, has motivated research to develop management strategies informed by the framework of community genetics.

The first study demonstrates that adding population regulation to a genetic model of spatially varying selection alters the prediction of the rate of evolution of resistance in the European corn borer (*Ostrinia nubi-*

lalis) to *Bt* maize. The second study focuses on the effect of natural enemies on the evolution of resistance in the same system. Differential egg mortality rates on resistant and susceptible genotypes of corn borers are mediated by differences in oviposition rates in *Bt* and non-*Bt* maize fields caused by restricted movement of females and by density-dependent responses of predators. This has the potential to affect the rate at which resistance evolves.

The third study addresses the effects of habitat fragmentation on the persistence of previously extensive populations of long-lived, self-incompatible plants (*Echinacea angustifolia*), as found in the North American tallgrass prairie. Habitat fragmentation is often modeled in a purely ecological framework (e.g., Nee and May 1992). We demonstrate that explicit consideration of the genetic basis of the plant mating system (Bataillon and Kirkpatrick 2000, Glemen et al. 2001) more fully reveals the consequences of fragmentation and suggests approaches to promoting persistence of the remnant populations.

The fourth study concerns the evolutionary interaction between a host plant (maize) and its pathogen (corn smut, *Ustilago maydis*) after a massive range expansion of the host species following domestication. This system exhibits remarkably durable resistance, contrary to the commonly observed accelerated evolution of virulence in agricultural monocultures. Such an evolutionary "cold spot" might be caused by historical biogeographic and contemporary genetic factors.

NONEQUILIBRIUM DYNAMICS

Evolution of resistance to transgenic Bt crops

Transgenic *Bt* crops have been developed by inserting a gene that codes for a crystalline protein (Cry toxin), which is selectively toxic to some insects, from the soil bacterium *Bacillus thuringiensis* (*Bt*) into the genome of a crop. Presently, potato, cotton, maize, broccoli, cabbage, canola, eggplant, poplar, soybean, rice, tobacco, and tomato have been transformed to express a Cry toxin, but only *Bt* cotton and *Bt* maize are now commercially grown in the United States. At least nine different types of Cry toxins have been used in crops that have been commercialized in the United States, each with its own unique toxicity spectrum and pattern of expression. Many of these *Bt* crops are very effective at killing target pests, in many cases allowing <0.1% survival in field conditions (Andow 2001).

Transgenic crops have stirred passions both for and against them, drawing attention to scientific investigations into their potential environmental and human health risks (NRC 2002). One of the significant environmental risks associated with these plants is that the target pests will evolve resistance to the Cry toxins, rendering the *Bt* crops ineffective (Tabashnik 1994, Gould 1998).

TABLE 1. Frequencies and relative fitness of the genotypes in the two patch types. *S* is a susceptible allele, *R* is a resistant allele, and *p* is the frequency of the *R* allele.

Measurement	Genotype		
	<i>SS</i>	<i>RS</i>	<i>RR</i>
Frequency (patch 1, toxic)	$(1 - p)^2$	$2p(1 - p)$	p^2
Frequency (patch 2, refuge)	$(1 - p)^2$	$2p(1 - p)$	p^2
Relative fitness (patch 1)	<i>k</i>	$Lh + k(1 - h)$	<i>L</i>
Relative fitness (patch 2)	1	$\kappa\eta + (1 - \eta)$	κ

Notes: Genotype frequencies are for a randomly mating population. Relative fitness in the toxic field is related to the ability of the genotypes to survive the toxin, and generally, $k \ll L$. Here *h* determines dominance of resistance, with $h = 1$ for completely dominant resistance and $h = 0$ for completely recessive resistance. Relative fitness in the refuge is related to the cost of resistance, with κ the cost to the *RR* homozygote and η the dominance of the cost.

The study of the evolutionary dynamics of resistance evolution began with Melander (1914), but it was Comins (1977) who developed a mathematical model incorporating selection and population dynamics. Since that time, additional mathematical (May and Dobson 1986; Ives and Andow submitted) and simulation (e.g., Tabashnik 1994, Alstad and Andow 1995, Gould 1998, Hillier and Birch 2002) models have added to our understanding of resistance evolution (for a concise review, see Rausher [2001]). All of these models are patch models, with a toxin selecting for resistance in one (or more) patches and no selection (or counter-selection) in the other patch (or patches). Although the results of these theoretical investigations are complex, the evolutionary dynamics depend largely on the genetic parameters (selection coefficient, dominance) and interpatch dispersal.

Here we focus on a simpler problem. To understand resistance evolution, it is necessary to have some kind of underlying genetic model, whether population genetic or quantitative genetic. For example, Levene's (1953) two-patch, niche-selection population model foreshadows Comins (1977), but does not treat population dynamics explicitly. It remains unclear what, if anything, a population dynamic component to the model adds to our understanding of resistance evolution and, more generally, of spatially varying directional selection.

A standard migration-selection population genetic model is described in Crow and Kimura (1970:267). This model has no population dynamics and has been used to understand how migration and selection can maintain genetic polymorphism. To clarify generally the role of population dynamics in directional selection problems, we use the Comins (1977) model with and without population regulation. Here patch 1 is exposed to the toxin and patch 2 is not exposed to the toxin; the relative fitness of the genotypes is given in Table 1. Complete mixing of genes among patches occurs between generations. Population regulation in this

model is determined by simple density dependence (Hassell 1975).

To reveal an effect of population regulation, we concentrate on a special case of resistance evolution, the high-dose plus refuge strategy, which now is used to delay resistance evolution in *Bt* crops in the United States (Alstad and Andow 1995). Under this model, the genetics of resistance are restricted to the case of recessive resistance and no cost of resistance. In addition, to simplify analysis, we assume that movement is random and that all individuals are redistributed at each time step.

The genetic parameters for the model are described in Table 1. One can show that if resistance is not over-dominant ($0 \leq h \leq 1$, where h is dominance), then the equilibria are the same for the model with and without population regulation. The resistant allele will go to fixation if the relative fitness of the resistant homozygote, L , exceeds the relative fitness of the susceptible homozygote, k ; the susceptible allele will go to fixation when the reverse holds. In these simple directional selection models, there are no novel equilibria when population regulation is added to a population genetic model. From an ecological perspective, however, the equilibria are only a part of the story. Indeed, for highly forced systems (Palumbi 2001b), they may be only a minor part of the story. It is through the nonequilibrium dynamics that the evolutionary process will interact most strongly with the surrounding ecological community, and it is to these nonequilibrium dynamics that we turn.

We denote the frequency of resistant alleles in the population by p . For rare, recessive resistance (p and h very small), the evolutionary dynamic of the Comins (1977) model can be approximated by a Taylor expansion. For the Comins model, lacking population regulation, a second-order Taylor expansion around $p = 0$ and $h = 0$ gives

$$\Delta p = \frac{(L - k)F_1(1 - Q)}{F_1k(1 - Q) + F_2Q}p(p + h) \quad (1)$$

where F_1 and F_2 are the fecundities in the *Bt* field and non-*Bt* field, respectively, and Q is the proportion of the refuge. This second-order approximation fits the full model until $p > 0.2$ and $h > 0.1$. However, when $p > 0.2$, resistance rapidly reaches fixation in the population, so for all practical purposes, the approximation is excellent. This approximation shows that resistance evolves at a faster rate with higher dominance (h) and resistance allele frequency (p). Recessive resistance (low h) evolves much more slowly than dominant resistance (higher h). The fraction in Eq. 1 is the reproductive advantage of the *RR* genotype (resistant homozygote) over the *SS* genotype (susceptible homozygote) in the toxic patch, relative to the reproductive rate of the *SS* genotype in both patches. Population density does not enter into the equation, and evolution does not depend on the population dynamics.

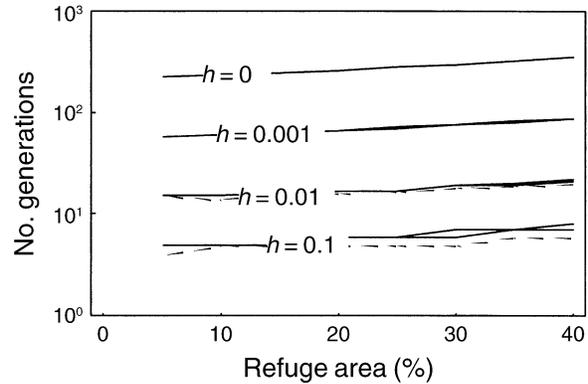


FIG. 1. Number of generations until control failure (i.e., resistance allele frequency = 50%) from the full Comins (1977) model and the second-order Taylor approximation (Eq. 2) vs. percentage of area planted as refuge for levels of heterozygote expression $h = 0, 0.001, 0.01$, and 0.1 , with random movement and high *SS* mortality ($k = 10^{-3}$). For each value of h , simulations were performed for different levels of “effective” reproduction in nontoxic fields; the lines are often coincident. Dashed lines give the predictions from the approximation.

The Comins (1977) model with population regulation yields different rates of evolution. The second-order Taylor approximation ($p = 0$ and $h = 0$) is derived by Ives and Andow (submitted) and is

$$\Delta p \approx (L - k) \left(\frac{x'_1}{x'_1 + x'_2} \right) p(p + h) \quad (2)$$

where x' is evaluated at $p = 0$; i.e., the various x' values are the population sizes of *SS* genotypes in the toxic and refuge patches. The second-order approximation fits the full population genetic model until $p > 0.2$ and $h > 0.1$ (Fig. 1). This is similar to Eq. 1, with the same dependence on h and p . However, when population regulation is added to the model, the proportion of the *SS* population that occurs in the toxic field also influences the rate of evolution. Compared to the model without population regulation, simple density-dependent population dynamics will alter the rate of evolution of resistance. We conclude that it often will be necessary to consider both the population dynamics and the genetic dynamics when investigating the rates of evolutionary change.

The directional selection model is one of the simplest models of evolutionary biology. The results we present here suggest that evolutionary rates will be different when simple density-dependent population dynamics are explicitly considered compared to a model without an explicit population dynamic. Hence, nonequilibrium dynamics may persist for longer or shorter periods of times and perturbations from equilibria may occur more readily or less readily compared to predictions from pure population genetic models. The model that we discuss here is a simplified directional selection model, with random movement and random mating and a rare

recessive allele. It is likely that more complex directional selection models will show even richer behaviors. If these results do generalize to more complex evolutionary models, ecological interactions among species within communities may have considerable influence on the pace of evolutionary change.

Natural enemies and the evolution of resistance

Because resistance traits have strong effects on herbivore mortality, development, and behavior, it follows that the herbivore's natural enemies will be indirectly (or directly) affected by these traits (Boethel and Eikenbary 1986). Reciprocally, members of the third trophic level, including predators, parasitoids, and pathogens, also affect the outcome of plant–insect interactions, including the rate of resistance evolution by herbivores to antiherbivore defenses of plants. A community genetics perspective helps us to understand how natural enemies may affect the rate of resistance evolution of herbivores to plant defenses because of the role that natural enemies can play in biasing the mortality of resistant vs. susceptible herbivore genotypes. Gould et al. (1991) suggested that natural enemies could lead to either an increase or a decrease in the rate of resistance evolution in herbivores, depending on the details of the herbivore–natural enemy interaction. The evolution of herbivore resistance will be accelerated if the attack on susceptible genotypes is disproportionately greater than the attack on resistant genotypes; conversely, the rate of resistance evolution will be reduced by disproportionate attacks on resistant genotypes (Gould et al. 1991, Gould 1994).

In the case of strong resistance (e.g., plants expressing high doses of *Bt* toxin), differential attack of resistant and susceptible herbivores will be mediated primarily by herbivore density (Gould 1994). The density of feeding-stage herbivores on *Bt* plants will initially be orders of magnitude lower than the density of feeding-stage herbivores on non-*Bt* plants. However, resistant individuals will form a much higher fraction of the herbivores feeding on the *Bt* plants than on the non-*Bt* plants. Thus, we expect a negative relationship between herbivore density and the frequency of resistant genotypes among feeding-stage herbivores. The question therefore becomes: are low-density herbivores at higher or lower risk of natural enemy attack than herbivores at high densities (Gould 1994; J. White, unpublished data)? A positively density-dependent attack rate implies lower risk at low densities, which would allow resistant genotypes to 'escape' from attacks by natural enemies in the *Bt* crop. The result would be accelerated resistance evolution. An inversely density-dependent attack rate, on the other hand, would imply increased risk at lower herbivore densities and a delay in the evolution of resistance, especially if the attack rate were inversely density dependent over a range of particularly low prey densities. Thus, the effects of natural enemies attacking feeding-stage herbivores on

the rate of resistance evolution will be inversely proportional to their relative impact on herbivores on toxic vs. nontoxic plants. If attack rates are greater on toxic plants, the rate of resistance evolution will be slowed, and vice versa.

The effects of egg mortality on resistance evolution are less transparent because the egg stage precedes selection based upon plant genotype. Indeed, Gould et al. (1991) suggested that the presence or magnitude of egg mortality should have no effect on the rate of resistance evolution of herbivores to plant toxins when herbivore oviposition rates are equal on toxic and nontoxic plants. But should we expect equal oviposition rates? At least two scenarios could lead to lower herbivore oviposition rates on toxic plants: (1) female choice, and (2) lower densities of ovipositing females in plantings of toxic plants. Female avoidance of plants engineered to express transgenic insecticidal toxins has not yet been documented. Lower densities of ovipositing females in plantings of toxic plants are likely, however, if these plantings are large and if female movement is at all restricted. In *Bt* maize, a key herbivore is *Ostrinia nubilalis* (Hübner) [Lepidoptera: Crambidae], the European corn borer. Because *Bt* fields generate far fewer adults of this species during its second-generation flight period than do non-*Bt* fields or refuges, the density of *Ostrinia* egg masses is lower in *Bt* maize (D. A. Andow and D. N. Alstad, unpublished data). It is therefore likely that *Ostrinia* egg masses will be present at lower densities in *Bt* vs. non-*Bt* maize and that this difference will be increasingly large as the size of *Bt* plantings increases. Under conditions of unequal oviposition rates in *Bt* vs. non-*Bt* maize, density-dependent egg mortality rates have an opportunity to influence the attack rates on eggs in the two habitats.

We constructed a population genetic model that allowed for positive density-dependent and inverse density-dependent mortality to act upon the eggs of an herbivore that is affected by a high-dose plant toxin in the larval stage. The model includes a nontoxic refuge and allows a fraction of females to oviposit in the same field in which they developed. Males are assumed to mate at random with females in both toxic and refuge fields. Simulations of the model show that if egg predators or parasitoids show a positively density-dependent attack rate, they impose disproportionately higher mortality in non-*Bt* fields, which accelerates the evolution of resistance to *Bt* maize in *Ostrinia* (Fig. 2). In effect, the *Bt* plants constitute a refuge from natural enemy attack and the reduced egg mortality exposes disproportionately more larvae to selection in the *Bt* fields (i.e., more resistant, but not susceptible, larvae would be allowed to develop). Alternatively, with inversely density-dependent egg mortality, the rate of resistance evolution declines (Fig. 2). Here, the refuge from natural enemy attack is in the non-*Bt* maize, where both resistant and susceptible larvae benefit. The model also shows that the level of egg mortality itself can

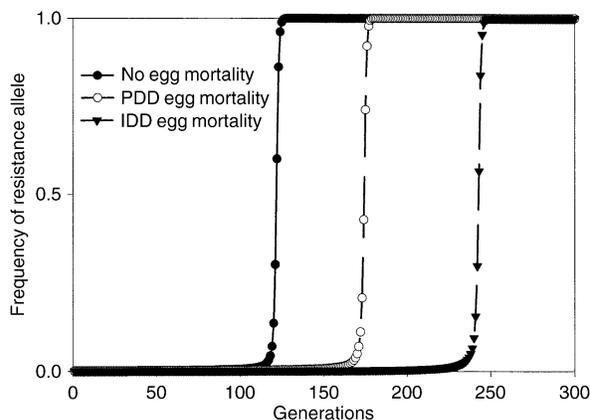


FIG. 2. Results of simulations illustrating the effects of different forms of egg mortality on the evolution of resistance of herbivores to high-dose insecticidal toxins in plants. Single-locus recessive resistance is assumed with an initial frequency of a resistance allele equal to 0.001. The area planted to toxic fields is four times the area planted to nontoxic fields, resulting in a 20% nontoxic refuge. One-fifth of the females oviposit in the same field where they developed as larvae, and the remaining females are distributed evenly across toxic and nontoxic fields. Egg mortality occurs prior to selection in the model and is simulated in three ways: (1) no egg mortality; (2) an egg mortality rate that increases with herbivore density by $N(i)/[k + N(i)]$, where k is a constant and $N(i)$ is the density of toxic or nontoxic plants (positive density-dependent egg mortality, PDD); and (3) an egg mortality rate that decreases with herbivore density by $1 - N(i)/[k + N(i)]$ (inversely density-dependent egg mortality, IDD). The constant k was set to equalize overall egg mortality rates in the PDD and IDD runs prior to fixation of the resistance allele. Herbivore fecundity was set at 100, and larvae that survive selection (or feed on nontoxic plants) are subject to density-dependent intraspecific competition.

influence the rate of evolution resistance, with higher rates of mortality slowing down the evolution of resistance.

We now turn to the natural enemies of *Ostrinia* eggs to evaluate if any are likely to cause density-dependent mortality. *Ostrinia* eggs are eaten by a number of egg predators that can collectively impose mortality rates of up to (and in some cases exceeding) 50% (Andow and Risch 1985, Andow 1990, 1992). The most important *Ostrinia* egg predators are the native lady beetle *Coleomegilla maculata*, lacewing larvae, and various predatory bugs (Andow 1990, 1992). The recently introduced multicolored Asian lady beetle, *Harmonia axyridis*, also feeds on *Ostrinia* eggs (Hoogendoorn and Heimpel 2002). *Ostrinia* eggs are subject to parasitism, but naturally occurring egg parasitism impacts <1% of *Ostrinia* eggs over most of the species' North American range (Andow 1992). Augmentative releases of native and introduced *Trichogramma* spp. can cause substantial egg mortality, but these releases, for the most part, have not been considered economically feasible, in part because multiple releases have to be made each year (Smith 1996, Andow 1997). Recent work with an egg parasitoid recently imported from northeastern China

(*T. ostriniae*) suggests, however, that only a single release is needed early in the season, making it more likely that releases may become economically viable (Wright et al. 2001, 2002).

Do egg predators or parasitoids show density-dependent responses (either positive or negative) to *Ostrinia* egg density? Predators of European corn borer eggs are generalist feeders that typically also utilize aphids, other arthropods, and corn pollen in addition to European corn borer eggs (Andow 1996). Predation on *Ostrinia* eggs depends on the community composition of alternative prey, so that the response to egg density is indirect and complex (J. Harmon, unpublished data). Parasitism of *Ostrinia* eggs by *T. ostriniae* appears to be density independent at low host densities and inversely density dependent at higher egg densities (Wang and Ferro 1998). Like other parasitoids, *T. ostriniae* presumably can become limited by the number of eggs that they carry or by handling time if host densities get high enough (Getz and Mills 1996, Rosenheim 1996, Heimpel and Rosenheim 1998). If *Ostrinia* egg densities are high enough to induce egg or handling-time limitation in non-Bt maize and low enough for these factors not to come into play in Bt maize, then egg parasitism could indeed be higher in Bt maize, with a concomitant reduction in the rate of evolution resistance in *Ostrinia*.

Habitat fragmentation

Habitat destruction and resulting fragmentation are major causes of species extinctions. Investigators concerned about the persistence of remnant plant populations have documented ecological and genetic effects of habitat fragmentation (Leach and Givnish 1996, Young et al. 1996, Newman and Pilson 1997). To obtain a community genetics perspective on the interplay of these effects, we have incorporated the empirical results of Wagenius (2000) on *Echinacea angustifolia* (Asteraceae), the narrow-leaved purple coneflower, into an individual-based, spatially explicit, stochastic simulation model. *Echinacea angustifolia* is native to the North American tallgrass prairie, which has been reduced to isolated fragments in a matrix of agriculture during the past 150 yr. Contrary to the results of a purely ecological model, we find that the genetic properties of our study system exacerbate the risk of extirpation.

Echinacea angustifolia shares five key features with many of the plants that formerly dominated unbroken prairie: (1) long life (*Echinacea* is a long-lived perennial and plants rarely flower before their third year); (2) reproduction strictly by seed (*Echinacea* does not spread vegetatively, so regeneration of populations depends exclusively on seed production); (3) self-incompatibility (seed set from each floret depends on receipt of pollen from another plant; McGregor [1968], Leuszler et al. [1996], Franke et al. [1997]); (4) pollination by generalist insects (service by nonspecialized pol-

linators is likely to limit flights for pollen or nectar to short distances; Kunin [1992]); (5) no specialized mechanisms of seed dispersal (*Echinacea* seeds are unlikely to colonize distant habitat patches). These features of *Echinacea* make it a suitable model for the conservation of many native perennial plants.

In a 6400-ha study area of western Minnesota farmland, Wagenius (2000) mapped >2000 *Echinacea* plants in 48 remnant populations varying in size from one to several thousand flowering individuals. He found that pollen limitation increases with the isolation of individual plants and that pollen limitation reduces seed yield. He also found that plants grown from seeds collected in small populations are less vigorous than those from large ones. Each of these findings could result from ecological or genetic processes.

Ongoing research tests ecological and genetic hypotheses about the causes of pollen limitation and reduced vigor. Two non-exclusive processes could influence pollen limitation. An ecological hypothesis holds that isolated plants receive fewer visits and, consequently, less pollen from pollinating insects than non-isolated plants because of restrictions on pollinator flight. According to a genetic hypothesis, plants receive similar amounts of pollen regardless of their isolation, but isolated plants receive a greater proportion of incompatible pollen from related plants that share self-incompatibility alleles than do non-isolated plants. Preliminary results do not support the ecological hypothesis. However, there is evidence that the receipt of incompatible pollen varies with isolation; mating incompatibility rates are now being assessed in small and large fragments. Similarly, two factors might influence plant vigor: under an ecological hypothesis, aspects of the abiotic environment (such as the fire regime) or biotic environment (such as abundance of exotic plants) differ in small and large remnants. Under a genetic hypothesis, genetic composition differs between small and large remnant populations. Not surprisingly, plant vigor varies with both ecological and genetic factors.

To assess how the interplay of the ecological and genetic processes affects population persistence, we developed an individually based, spatially explicit, stochastic simulation model. The model builds on previous models of habitat fragmentation and incorporates additional processes that affect population growth and persistence: density-dependent mortality, seedling recruitment as a function of the fire regime, and dispersal of pollen and seeds, as well as heterozygosity, as functions of local *Echinacea* abundance.

The simulation model demonstrates that a purely ecological framework is insufficient to predict the consequences of habitat fragmentation in our system. The purely ecological framework is based on Levins' (1969) metapopulation model, which describes the fraction of occupied patches, $u(t)$, in an infinite patch model with global dispersal:

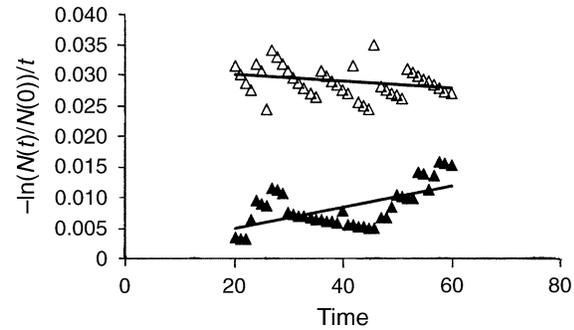


FIG. 3. Results of simulations on patch mortality as a function of time. The regression line for self-incompatible plants (solid triangles) shows a positive slope, indicating an increasing extinction rate due to reduced seed production caused by reduced availability of compatible pollen. The regression line for self-compatible plants (open triangles) shows a slope close to 0, indicating that patch mortality is constant over time.

$$\frac{du}{dt} = cu(1 - u) - eu. \quad (3)$$

Here, the parameter c denotes the colonization rate and e denotes the extinction rate of each patch. If a fraction D of the habitat is permanently destroyed, the model yields the following (Nee and May 1992):

$$\frac{du}{dt} = cu(1 - D - u) - eu. \quad (4)$$

It follows that the fraction of occupied patches in equilibrium is given by

$$\hat{u} = 1 - D - \frac{e}{c} \quad (5)$$

implying that the population dies out if the fraction of destroyed habitat D exceeds $1 - e/c$.

The model in Eq. 4 assumes that both the colonization rate and the extinction rate of a patch remain unchanged after habitat destruction. (Similar assumptions are made in the theory of biogeography.) Neither assumption holds: colonization depends on reproductive output, which decreases with fragmentation due to reduced availability of compatible (unrelated) plants. Likewise, persistence depends on reproductive output and individual survival, both of which are compromised when individual fitness declines with inbreeding in small remnants (Newman and Pilon 1997). For these reasons, we include genetic components in our model, varying the number of self-incompatibility alleles and the rate of inbreeding, to predict the fate of the remnant populations. In the simulation, we initially run the model without habitat fragmentation until an equilibrium is reached. A fixed fraction of the habitat is then destroyed and the fate of the patches is followed. Considering self-incompatibility alone, we find that the probability of extirpation increases over time (Fig. 3). Standard ecological models assume a constant patch

extinction rate and thus cannot predict this trend. Therefore, standard ecological models overestimate the persistence of remnant populations. Ongoing work is exploring the further consequences of inbreeding in the context of habitat fragmentation.

Habitat fragmentation poses threats from mechanisms as diverse as increased mating system incompatibility and reduced fire frequency. The community genetics perspective considers the joint consequences of these aspects of fragmentation, promoting understanding of how ecological and evolutionary processes together affect population persistence.

Domestication as invasion

Beginning <150 yr ago, vast acreages of temperate forests and grasslands in North America were converted to agricultural production, and in that process, novel crop plant genotypes were introduced (Smith 1989). In North America, the conversion to modern maize arguably represents one of the largest plant range expansions within human history. Although the impact of agricultural conversion on the landscape is readily apparent, the impact on plant pathogens and the coevolution of plant and pathogen is less apparent, but no less important. We focus on possible effects of the rapid geographic expansion of maize and its associated fungal pathogen, *Ustilago maydis*, corn smut.

The maize–smut interaction is ideal for the study of coevolutionary dynamics under nonequilibrium conditions because genotypes of both species can be manipulated and the population history of maize is well understood. The transition from small, genetically variable teosinte populations of Central America to the large, monotypic maize plantings of North American agriculture is expected to accelerate the evolution of virulence in associated maize pathogens. *U. maydis* is a naturally occurring pathogen on both teosinte and maize (Duran 1987) and has tracked maize from domestication to present-day plantings. The history of maize domestication and spread are well documented (Galinat 1992), as is the molecular genetic basis of its evolution from teosinte (e.g., Doebley 1992, Hilton and Gaut 1998). Virtually every maize plant grown in North America has a recorded pedigree, but much less is known about *U. maydis* evolution. Historical records show that maize breeding programs for smut resistance of the early 1900s were successful; surprisingly, the pathogen has not evolved to overcome smut resistance traits developed at that time (Christensen 1963), and smut resistance in maize has proven durable over 50 yr. Our long-term goal is to account for the difference between the observations of low levels of smut infection on widely planted corn varieties and an expectation for rapid evolution of virulence in agricultural monocultures. More immediately, we ask how maize domestication and geographic range expansion have affected the population genetic structure of *U. maydis*.

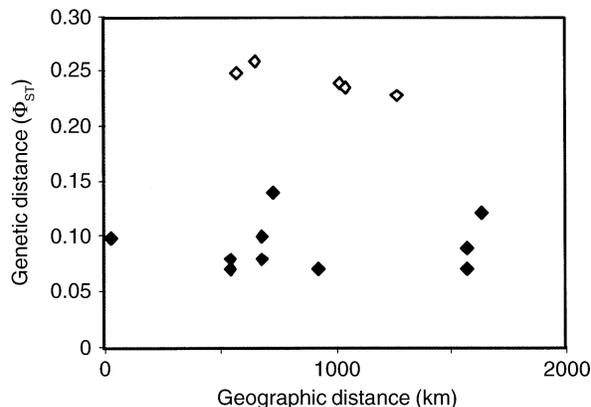


FIG. 4. Correlation of genetic (as Φ_{ST} values) and geographic distances in pairwise comparisons of North American populations of *Ustilago maydis*. Open symbols show pairwise comparisons between Ohio and other North American populations. The Φ_{ST} levels from pairwise comparisons show no correlation with distance, using a Mantel test ($rY = -0.006$, $P = 0.35$; Schneider et al. 1997).

Seven North American populations of *U. maydis* were sampled from field corn and sweet corn, and genetic relatedness of the populations was assessed using 11 genomic probes for restriction fragment length polymorphisms (RFLPs). Using Φ_{ST} , a multilocus analog (Schneider et al. 1997) to Wright's inbreeding coefficient, F_{ST} , genetic variation within and between North American populations was estimated. Values for Φ_{ST} varied from 0.07 to 0.26 across pairwise comparisons of these populations. Overall levels of heterozygosity are quite high (~ 0.4) and estimated levels of inbreeding within one population are low ($F_{IS} \sim 0.06$), despite the fact that sib matings could occur. Using an Index of Association test (Agapow and Burt 1999), analysis of linkage disequilibrium revealed that the alleles demonstrating significant association between loci within populations were not the same in all sampled populations. In contrast to the population genetic structure observed for many crop pathogen species (e.g., Boeger et al. 1993), we did not observe isolation by distance (Slatkin 1993), as one might expect with wind-borne dispersal of spores and high migration rates (see Fig. 4). Together, these data demonstrate that *U. maydis* populations are sexually reproducing and maintain high levels of heterozygosity, distributed unevenly among genetically variable populations across the major geographic regions in which maize is grown (J. Garton and C. Ramos, unpublished manuscript).

We developed two hypotheses to explain our observations. (1) The variation that we observe across smut populations reflects historical founder events as maize was brought into North America about 1000 yr ago. These populations have not come to equilibrium by genetic drift and migration. (2) The genetic variation among smut populations is the result of host or regional environmental selection effects (e.g., Ahmed et al.

1996). These are not exclusive hypotheses. To generate expectations for historical sampling effects alone, in collaboration with Frank Shaw, we modeled the process of establishing North American descendant populations. All observed variation was placed in an “ancestral urn” of Central America and alleles were drawn to found new descendant populations, without migration among descendants. The model is comparable to assuming that smut was brought in with the introduction of the crop, but that little migration between populations subsequently occurred. We used data for the self-incompatibility locus of the fungus, *b*, for which 18 alleles are described and occur in approximately equal frequencies due to balancing selection (Zambino et al. 1997). Thus, each allele would have an approximately equal chance of being sampled from the ancestral population and, upon arrival in a new population, would be less likely to be lost due to drift. The draws were independent of each other and we assumed that the source population was large enough so that sampling with replacement was a good approximation (binomial sampling). Using this model, we constructed a statistical test based on comparing the empirical observations for the occurrence of *b* alleles in subpopulations (Zambino et al. 1997) with those obtained from the simulation model. The simulations were carried out with 5, 20, and 100 descendant populations and with the number of alleles drawn varied at 3, 5, 10, 20, and 30. Each combination of parameters was repeated 1000 times. Our simulation results do not allow rejection of the null hypothesis that the distribution of *b* mating-type alleles in current populations were determined by historical, random draws from an ancestral population. However, the statistical power is low in this chi-square test.

The second selection hypothesis is suggested by the data for the Ohio population, which displays pairwise Φ_{ST} values (~ 0.24) twice those for other pairwise comparisons in North America (see Fig. 4). In the mid-1900s, breeding for smut resistance was conducted at the research station from which collections were made. Further, pairwise comparison of the North American populations with one Uruguay collection suggests that selection due to host genotype or other regional environmental factors could have a large impact over a short time. We observe high Φ_{ST} (~ 0.4), values typically associated with differences between species, yet the Uruguay and North American populations can only have been separated by a period of 4000–5000 yr. Altogether, our data suggest that relatively large or diverse populations of smut arrived in North America with maize, and that insufficient time since the introduction (≤ 1000 yr) has elapsed to distribute that variation evenly across the widespread maize plantings.

Remarkably, then, the current populations of smut in North America might be the “footprints” of early introductions rather than the result of high migration rates that we often associate with agricultural patho-

gens (Burdon and Silk 1997). To now resolve the relative importance of historical founder events and strong selection in establishing the observed patterns of genetic variation in *U. maydis* populations, we will combine experimental population approaches, models, and sampling in geographically diverse locations, especially Central America. Our results to date suggest that the pathogen population in North America is primarily outcrossing and sexual, rather than inbreeding or clonally reproducing. Such a pathogen reproductive system, combined with the quantitative resistance in maize (e.g., Lubberstedt et al. 1998), may contribute to the strikingly slow evolution of virulence in this pathogen’s populations. Lack of correspondence between pathogen virulence and host resistance structure has previously been attributed to the patchy distribution of genetically variable host plants and environment (Burdon et al. 1989, Clarke et al. 1990, Jarosz and Burdon 1991, Burdon and Silk 1997) and to the cost of resistance (Bergelson and Purrington 1996). If additional studies reinforce our view of the evolutionary interaction of maize and its very common pathogen, corn smut, we might add a third factor. Could history and the genetic structure of the maize–smut interaction conspire to make an evolutionary “cold spot,” analogous, but opposite in outcome, to Thompson’s (1999) evolutionary “hot spots”?

DISCUSSION

Community genetics jointly considers genetic and numerical dynamics of interacting populations to yield fresh insight into evolution within the context of communities. We demonstrated the value of a community genetics approach for studies characterized by nonequilibrium dynamics in which strong interactions act on genetic variation. Nonequilibrium situations are common now; anthropogenic disturbances impose strong selection regimes on many natural and managed communities. Indeed, unmanaged natural communities are increasingly scarce and management itself can be a large disturbance. In addition to the fundamental insights that community genetics offers, its approaches become more compelling as the human impact on the landscape mounts. Principles that we derive from such studies will be valuable in sustainable management of resources, conservation genetics, and urban planning.

The idea that evolutionary change can occur on relatively short time scales is not new and can be traced back to work by Dobzhansky and others in the 1940s. For instance, Timofeef-Ressovsky (1940) and Dobzhansky (1943) demonstrated rapid evolutionary changes coinciding with seasonal cycles. Rapid evolutionary changes can also occur in a static abiotic environment as a result of dynamic interactions among organisms within a community, as predicted in the Red Queen model and its derivatives (Van Valen 1973).

A community genetics perspective can bring novel insight not only to nonequilibrium situations such as

we discuss here, but also to the case of equilibrium dynamics with strong balancing selection. For instance, Antonovics (1992) investigated a model of host–pathogen interactions, in which he demonstrated that the observed coexistence of susceptible and resistant plant genotypes was only consistent with a model that combined ecological and genetic dynamics. We focused on nonequilibrium situations because they are more likely to produce pronounced effects of interactions. The four studies in this paper demonstrate (1) that an ecological or an evolutionary framework by itself is insufficient to understand or predict outcomes of organismal interactions during the transient phase following perturbation, and (2) that novel predictions about community change can emerge from mathematical models that incorporate both ecological and genetic processes. Only when we consider both factors in concert can we understand community dynamics following a large perturbation that imposes strong selection on the community. In each of the studies that we discussed, strong selection occurs naturally; it is characterized by an abrupt and large change that imposes strong selection on the community. The transient phase to equilibrium may be long lasting and, with increased human impact, an equilibrium may never be reached.

We believe that our examples are illustrative of the common phenomenon of nonequilibrium conditions in contemporary communities. Agricultural and forested areas, which cover over half of the earth's terrestrial area, are subjected to massive ecological and evolutionary disturbances, generating nonequilibrium dynamics within those habitats, as illustrated in our first example of resistance evolution. These same activities generate nonequilibrium dynamics in native habitats by fragmenting and isolating these habitats, which we illustrated in our example of patch dynamics in prairies.

We recognize that many of our examples involve only two-species “communities.” We have chosen to highlight these relatively simple interactions to lay bare the structure of community genetics and illustrate some of the necessary conditions under which it can truly matter. We suggest, however, that this focus does not limit the generality of our analysis. Indirect interactions in ecological communities appear to be common (Holt and Lawton [1994], Wootton [1994]; see also the companion paper by Whitham et al. [2003]). Hence, evolutionary change in two-species interactions has the potential to affect other members of the community through indirect species interactions. For instance, genetic variation in resistance to herbivores in plants can affect the herbivores' natural enemies (Price et al. 1980). Plant defenses reduce the fitness of predators and parasitoids of herbivores feeding on them (Campbell and Duffey 1979, Duffey et al. 1986, Obrycki 1986). Thaler (1999) also recently showed that the production of plant defenses is correlated with the production of volatiles that attract parasitoids of the herbivores feeding on the defended plants. In this case and

some others, the attraction of an herbivore's natural enemies appears to be a component of the plant's defensive reaction (DeMoraes et al. 1998, Bradburne and Mithen 2000). In examples such as these, one can envision evolution within entire multispecies complexes.

The importance of taking a combined ecological and evolutionary approach to understand the effects of large-scale perturbations was recently emphasized by Palumbi (2001a) in a *Science* article entitled “Humans as the World's Greatest Evolutionary Force” (see also Palumbi 2001b). The rapid growth of the human population has led to unprecedented alterations of natural ecosystems and widespread introduction of novel organisms. Consequences of human impact are felt in all areas, including epidemiology (emerging diseases, resistance to antibiotics), pest management (evolution of resistance to pesticides), species invasions (globalization, homogenization), species extinctions (habitat fragmentation, climate change), and expansion of agricultural land (to destroy natural habitats).

The magnitude and spatial extent of disturbances are staggering; no habitat seems to be fully protected. Coastal marine environments around the world have been massively perturbed by dredging, pollution, impoundments, and an astounding number of invasive species (Carlton 1999). Riparian habitats in remote mountains have been massively perturbed by removal of beaver, damming of rivers, recovery of beaver, and biological species invasions. In highly perturbed systems, ecological and evolutionary forces are equally important.

A community genetics perspective relying on a theoretical framework not only leads to a more complete understanding of the consequences of human-induced selection pressure, but also provides a sound basis for the development of management strategies. Developing a unified theoretical framework is of paramount importance because our actions induce both ecological and evolutionary change. Without such a comprehensive framework, our understanding of the complexity by which communities and ecosystems respond to our actions will be severely compromised, and we will never be able to develop general management strategies to address these responses.

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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-

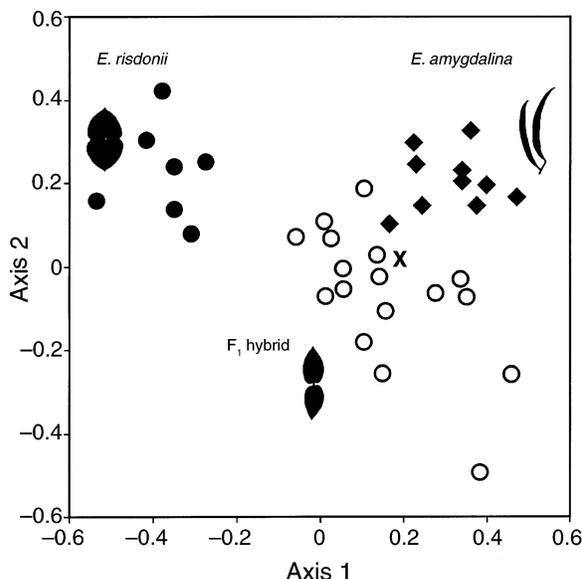


FIG. 1. In common-garden trials using crosses of known pedigree, F_1 hybrids accumulated the arthropod communities of both parental species, suggesting a heritable component to community structure. Each point represents the arthropod community of 30 insect taxa found on a family of trees, based upon 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-dimensional 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.

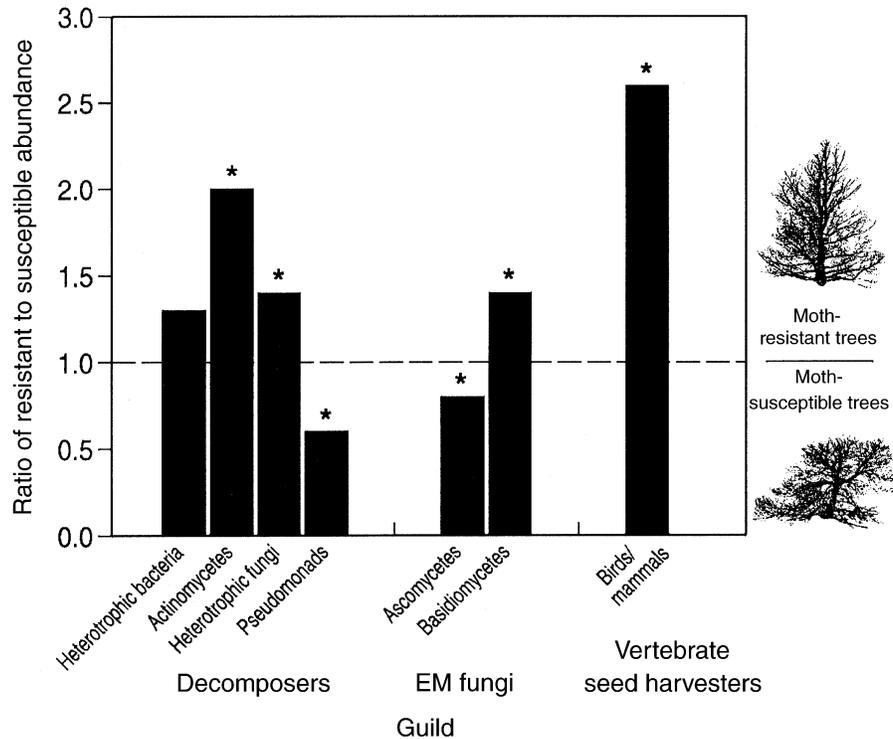


FIG. 2. Genetic variation among pinyon pines (*Pinus edulis*, a community dominant) in resistance to a keystone herbivore (*Dioryctria albiovittella*, a stem-boring moth) affects bird, mammal, and rhizosphere microbe communities. The graph shows the ratio of the abundance of seven guilds on resistant 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

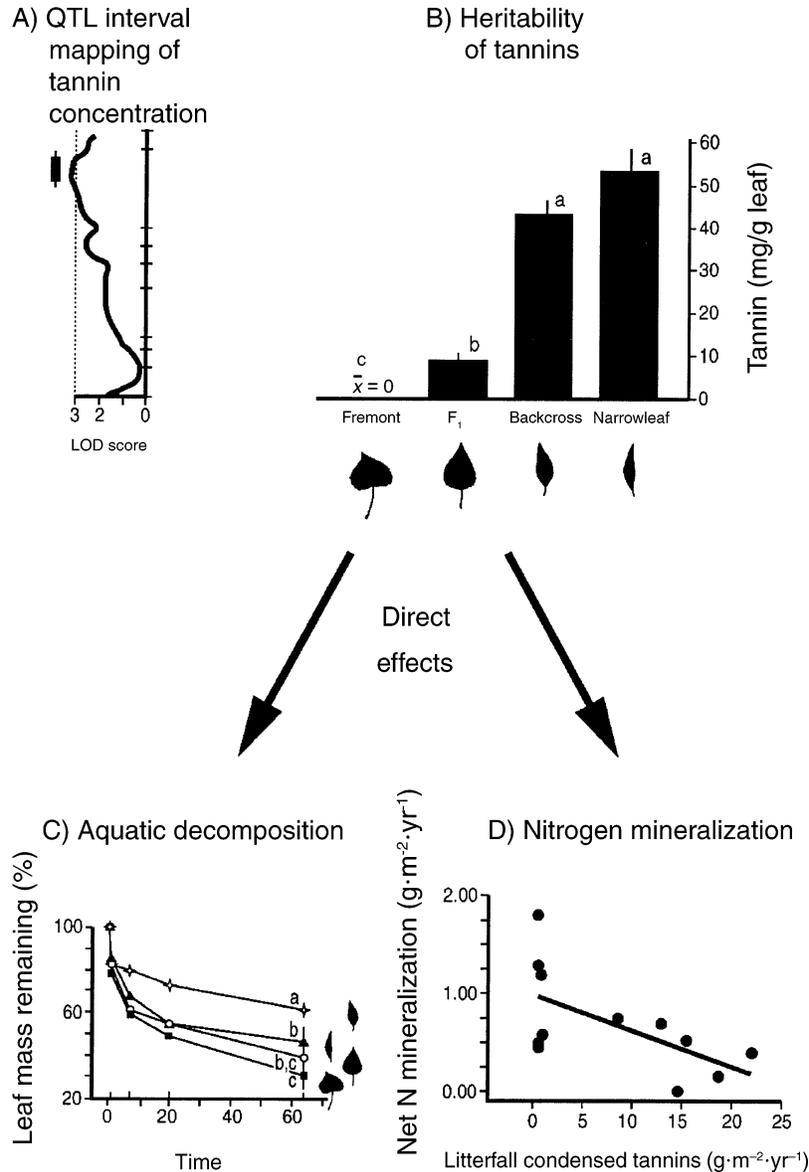


FIG. 3. Genetic variation in *Populus* hybrids results in differential expression of a condensed tannin QTL (Quantitative Trait Locus) that can be traced through ecosystem-level processes. (A) Composite interval mapping shows the location of a QTL for tannin concentration on a linkage group of a *Populus 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

$$w = b_{wz:zij \cdot zi \cdot zijk} + b_{wzj \cdot z \cdot zi \cdot zij} + b_{wzi \cdot z \cdot zi \cdot zi}$$

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, $b_{wz:zij \cdot zi \cdot zijk}$ 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 $b_{wzj \cdot z \cdot zi \cdot zij}$ 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, $b_{wzi \cdot z \cdot zi \cdot zi}$, 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 $z_{i \cdot}$, 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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WHAT CAN WE LEARN FROM COMMUNITY GENETICS?

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INTRODUCTION

Throughout the 20th century, investigators argued that genetics should be incorporated into ecological explanations (Collins 1986). C. C. Adams (1915) suggested very early in the century that emerging concepts in Mendelian genetics could help ecologists to explain the distribution of land snails in the genus *Io*. Genecology developed from 1920 to 1950, with research focused on intraspecific variation that anticipated ecological genetics, which developed in the 1950s and 1960s. Evolutionary ecology emerged in the 1960s, driven by empirical results in three areas (Collins 1986): ecologically significant traits like competitive ability had a genetic basis; some kinds of evolutionary change progressed within the time required for many ecological process to reach completion; and, natural selection operated over spatial scales sufficiently small such that microevolution partially explained the distribution and abundance of populations over relatively short distances. By the late 1960s, ecologists were also becoming increasingly sensitive to the level of analysis at which natural selection was expected to operate. Futuyma (1986:307) integrated these ideas in defining evolutionary ecology as “the analysis of the evolutionary origin of ecological phenomena with an explicit recognition of the distinction among, and the consequences of, selection at various levels (gene, organism, kin group, population, or higher).”

While on sabbatical at Duke University in 1982, I discussed population genetics and ecology with Janis Antonovics as I worked on a study of the history of the integration of ecology and evolutionary theory leading to the emergence of evolutionary ecology (Collins 1986). My efforts to understand the intellectual issues that drove the integration led to the question: To what extent is the genetic composition of populations in a community a function of the other species comprising the community? Antonovics (1992) outlined a research program in community genetics that began to address this question.

The papers for this Special Feature are the most recent use of genetics in ecology, but community genetics prompts a certain optimism for two reasons. First, as Neuhauser et al. (2003) show, our ability to model these interactions is improving. Advances in computational

biology will prove immensely useful for exploring the intersection of genetics, ecology, and evolution. Second, advances in genomics will hasten the day when we can document the genes in each individual that are responding to other organisms. In a manner analogous to studies, especially in the 1950s, that delimited ecosystems by tracing the paths of radioisotopes, a map of the genetic bases of ecological interactions will define a community. We are closing in on this possibility.

“Community genetics” is a neologism, and although the papers in this Special Feature present new advances, they also address classic questions in ecology. When, how, and why should genetics and evolution be incorporated into ecological explanations? Neuhauser et al. (2003) say a great deal about this question. Whitham et al. (2003) raise again the old question, “What is a community?” They also raise the more recent question, “Should we expect selection to act often at levels above the individual, including the community?” Both papers led me to ask: “What can these studies in community genetics tell us about how we do ecology?”

WHY COMMUNITY GENETICS?

Neuhauser et al. (2003) focus on non-equilibrium systems and understanding population and community dynamics over short time scales. For them, a community is a set of interacting species that may or may not have been together for very long. Their cases have the following important quality: a prediction about the outcome of interactions might be false unless the analysis assumes that the interactions may lead to gene frequency changes, hence evolution, in one or more of the species involved. Conceptually, then, community genetics has an important place within ecology. Neuhauser et al. care most about what is happening “in practice.” Their four leading examples are from human-dominated systems: evolution of resistance to transgenic *Bt* crops; natural enemies and the evolution of resistance; population persistence and the interplay of habitat fragmentation with genetics; and domestication as invasion. These are important examples in light of human-accelerated evolution (Palumbi 2001), especially in human-dominated urban environments (Collins et al. 2000). Their models show nicely that without population regulation, simple density-dependent population dynamics will alter the rate of disease resistance; i.e., predictions about population dynamics differ when genes are included or excluded. They generalize this result and conclude that ecological interactions among species in communities may accelerate

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the pace of evolution. The four cases illustrate how ecological theory related to communities is incomplete if it does not account for the fact that ecological and evolutionary processes jointly affect community dynamics.

Whitham et al. (2003) focus on equilibrational systems composed of species where interactions have evolved over a long time. The interactions have a genetic basis at the individual level, and the authors also argue (p. 568) that, "These interactions ultimately lead to genetically distinct communities, whose differences are detectable as the among-community component of variance in individual trait expression." The claims that "selection acts on genetic differences *at the community-level*" (italics theirs), and "community-level selection is widespread" are provocative, and if supported, have important implications for how we conceive of communities.

Neuhauser et al. and Whitham et al. also discuss the usefulness of community genetics for developing conservation strategies in a rapidly changing world. Several recent reports add to the mounting evidence of global warming. Fitter and Fitter (2002:1689) have concluded that, "... large interspecific differences in this response [to increasing temperature] will affect both the structure of plant communities and gene flow between species as climate warms." As we move from a focus on conserving individual species to conserving communities and ecosystems, it will be important to understand what we must do to retain interactions among organisms, interactions expected to have a genetic basis.

WHAT IS A COMMUNITY?

For Neuhauser et al. (2003), studying interspecific interactions must include genetics and the possibility of evolutionary change in order to predict a system's future state. This raises the question, "What is a community?" Relevant here is the issue of how long a group of species must associate if genetics and evolution are to matter. Neuhauser et al. claim that the association of a group of species need only be brief, placing them in a community ecology tradition that originates with Gleason (1917) and that found further expression in the 1960s when ecologists studied *Drosophila* communities, diatom communities, and bird communities. At that time, "ecologists departed from the functional definition of the community to a rather arbitrary concept that defines the community as the group of organisms being studied." (Wilbur 1972:3). This differs from a view in which the long-term proximity of species leads to many coevolved interactions and a network of species that, in an extreme, might express one or more traits at the community level that can serve as a basis for selection. Whitham et al. (2003) subscribe to this latter view, which places them at the other end of a continuum relative to Neuhauser et al. (2003).

Whitham et al. outline a more provocative program than Neuhauser et al., and it is one with more pitfalls. Whitham's team is interested in multilevel selection and community evolution. For them, a community is an equilibrational assemblage of organisms whose structure is heritable. They propose analyzing the genetic mechanisms at the root of what they envision as the community's extended phenotype, and they argue that the "transmission of extended phenotypes from one community generation to the next is powerful evidence that community structure is heritable." This is an important claim because, for them, the expectation that selection acts above the individual level means that community evolution is likely. If true, their argument would support the now rarely held view that ecological communities are analogous to superorganisms (Odum 1969), a position that also runs counter to the expectation of the neutral argument (Bell 2001, Hubbell 2001) that communities are "open and easily invaded" (Whitfield 2002:480).

At the heart of Whitham et al. is the assumption that organisms matter, natural history matters, and individual species matter. For this team, the theory on which our understanding of communities as organismal assemblages rests must incorporate genetics and evolutionary biology. Many of us would agree to this point. But they go on to argue that communities are a complex network of co-evolved relationships that support selection above the individual level. Many of us would disagree here. Their view raises issues related to levels of selection that are addressed by many including Wade (1978), Wilson (1980), and Williams (1992), as well as philosophers of science like Hull (1980), Sober (1984), and Brandon (1990). Whitham et al. must identify a community-level trait that is under selection to distinguish selection of genes at the individual level from selection for a trait at the community level. Gene frequencies can change by virtue of the life or death of groups, but that is not necessarily the same as selection for a group or community trait (Sober 1984).

WHAT CAN THESE STUDIES IN COMMUNITY GENETICS TELL US ABOUT HOW WE DO ECOLOGY?

The papers in this Special Feature are end points. For Neuhauser et al., communities can be loose amalgams of species that can evolve quickly, whereas Whitham et al. see communities as co-evolved networks of species that take time to develop. Throughout the 20th century, ecologists struggled to answer the question, "What is a community?" Among other things, community genetics provides a basis for investigating how the interactions among species might be more than just a series of encounters among organisms with similar physiological requirements. If the interactions among organisms living in the same habitat are evolved responses to other species in that habitat, then this interspecific genetic network can be the basis for defining a community in a manner analogous to the intraspecific

genetic network that delimits a population as a collection of individuals of the same species united by a common gene pool. Rapidly evolving genomic methods, such as microarray technology, may soon make it possible to employ this definition of a community using the genetic bases of interactions.

Community genetics integrates ecology and genetics and, hence, evolution. Ecologists often envision the diversity of a community as controlled by resources. The leading question becomes, "Based on resource availability, is there an empty niche that could be filled by yet another species?" For evolutionary biologists, diversity is a product of gene–development–environment interactions that produce novel phenotypes, but the *sine qua non* is just the right sort of genetic variation. At the recent Annual Meeting of the ESA, Roughgarden (2002) characterized these very different views as ecology setting the context for evolution while genetic variation sets the opportunity.

It is possible to integrate these views by imagining a "vacant niche" with sufficient resources to support a new species, and the subsequent evolution of a novel phenotype to fill the niche. However, Lewontin (1978) makes it clear that genetic variation is finite, and we can easily imagine "unoccupied niches" with no species ready to fill them; for example, there are no grass-eating snakes. Do these alternative explanations for how community diversity evolves matter for community genetics? They might. The food web configurations that we predict should be stable (*sensu* Pimm 1982) might not occur in nature, for two reasons: because the habitat is inaccessible to one or more of the species that could result in a stable assemblage; or, based on the kinds of organisms already present in a habitat, one or more species with the qualities needed to confer stability will not evolve because no populations have the necessary genetic variation. Pimm (1982) did not consider the effects of evolutionary change on food web structure because the consequences of such change within webs are complex; species interactions are not fixed, but can vary even to the point at which one species might shift roles from predator to prey or vice versa; and change in food web composition may be much faster than the rate at which populations can evolve. Pimm (1982:193) concluded that "How evolution affects the functions of multispecies systems and further restricts their possible food web shapes is uncertain. It is likely to remain that way for some time." Community genetics offers a framework for understanding the evolution of multispecies systems. The rate at which human actions are changing the mix of species in many communities accelerates our need to understand the degree to which the interactions that define food webs, and that confer on them properties like stability and resilience, are products of ecology as well as genetic variation.

Finally, each of these programs uses a multidisciplinary and interdisciplinary approach to doing science

that is interesting in and of itself as a tactic for studying communities (Collins 2002). Both programs employ vertically integrated research strategies (genes to communities or ecosystems) that rely on the collective effort of teams of collaborators, not just individual investigators. Ecosystem ecologists often work in teams, but it is a style of doing research found less commonly among population geneticists, population biologists, and community ecologists. Collaborative research is seen increasingly as a way to break down larger, complex environmental problems (Collins et al. 2003). The papers by Neuhauser et al. (2003) and Whitham et al. (2003) illustrate how answers to larger questions in evolutionary ecology can be addressed fruitfully by teams of investigators with skills across a range of scientific disciplines and subdisciplines.

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COMMUNITY ECOLOGY AND THE GENETICS OF INTERACTING SPECIES

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INTRODUCTION

Neuhauser et al. (2003) and Whitham et al. (2003) importantly stress that the selective forces acting on populations are complex, nonlinear, and the result of multispecies interactions peculiar to the specific communities where populations occur. Obviously, all natural populations are embedded in multispecies communities of varying complexity. Population biologists can create and study single-species populations in theoretical or laboratory settings, often with fascinating and illuminating results (e.g., Lenski et al. 1991, Buckling et al. 2000, Kassen et al. 2000). However, natural populations must evolve in response to a diverse array of biotic and abiotic selective pressures in the context of complex communities. This crucial point is generally not stressed in elementary treatments of theoretical population genetics (e.g., Hartl 1980). Clearly, the traditional treatment of selection pressure in simple population genetic models as an invariant coefficient called “s” is a pedagogically useful, but ecologically unrealistic, oversimplification.

Understanding how evolution depends explicitly on the identities, densities, and genotypes of strongly interacting species in moderately complex communities is a major challenge (Antonovics 1992, Neuhauser et

al. 2003, Whitham et al. 2003). The key questions that I want to address in this commentary are: (1) which species need to be included, and (2) when does the application of community genetics improve our understanding of community patterns and processes? It is also important to keep in mind that although selection occurs in a community context, communities are not likely to be units of selection, except under exceptional circumstances (Gilpin 1975). For that reason, some closing caveats about terminology and concepts seem prudent.

WHICH SPECIES TO INCLUDE?

Both Neuhauser et al. (2003) and Whitham et al. (2003) focus on strong interactions among a limited set of species embedded in a larger community. This approach is similar in spirit to the idea of community modules that Holt (Holt et al. 1994, Holt and Lawton 1994) has championed as a way to make the bewildering complexity of natural communities more analytically tractable. Indeed, the very few empirical studies of interaction strengths that we have for natural communities (Paine 1992, Raffaelli and Hall 1996) suggest that most species interact strongly with few others, and that interactions with remaining species are weak or nonexistent. If these studies are at all representative of the broad range of communities where the distribution of interaction strengths remains unmeasured, it may be reasonable to ignore the formidable analytical problem of treating natural selection as a

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product of direct and indirect interactions in an entire food web. Instead, complex communities can be broken down into many modules of a few strongly interacting species, and community genetics can focus on the evolutionary consequences of those limited sets of interactions. Consequently, an emphasis on the community genetics of keystone species (Whitham et al. 2003) or species within limited community modules (Neuhauser et al. 2003) seems eminently reasonable.

It is worth pointing out that a focus on the strongest interactions as agents of selection may sometimes be misleading. Some ecological interactions are so strong that populations are driven rapidly to extinction before any meaningful genetic change can occur. The ongoing local extinctions of amphibian populations in response to newly emerging chytrid and viral pathogens illustrate one situation in which strong ecological interactions cause extinctions instead of rapid, observable evolutionary change (Dzszak and Cunningham 1999, Dzszak et al. 2000). Granted, in this case, the lack of any observable increase in resistance to pathogens on the part of the amphibians may reflect a lack of relevant genetic variation as well as an extremely strong interaction. We know from other examples of rapid changes in host resistance that natural enemies can be potent agents of natural selection (Ratcliffe 1959, Levin et al. 1977, Bohannan and Lenski 2000). More indirect, but nonetheless compelling, evidence for the importance of natural enemies as agents of selection comes in the form of numerous spectacular examples of chemical, behavioral, and morphological defenses against consumers (Morin 1999). Comparable evidence for interspecific competition as a strong selective agent comes from studies of the repeated convergent evolution of similar sets of *Anolis* ecomorphs in island faunas (Losos et al. 1998). Interactions with natural enemies, competitors, and mutualists are all likely to impose significant selective pressure on individuals in natural populations.

WHEN DOES COMMUNITY GENETICS IMPROVE OUR
UNDERSTANDING OF COMMUNITY PATTERNS
AND PROCESSES?

Many of the examples of community genetics described by Neuhauser et al. (2003) and Whitham et al. (2003) focus on interactions between plants and their natural enemies. The main goal of this section is to suggest some other fertile areas for research. The first of these considers ecological and genetic differences among populations of the same species that result from different selective forces imposed by the very different communities in which those species occur. Fauth (1998) has described one intriguing empirical example for populations of amphibians living in North Carolina, USA. Fauth used "common garden" experiments conducted in artificial ponds to show that even over very small geographic distances, populations of one frog species, *Bufo americanus*, differed strikingly in com-

petitive ability, in ways that apparently depended on whether they regularly interacted with a competitor, *Rana palustris*. Similarly, Kurzava and Morin (1994) showed differences in the impacts of two subspecies of the predatory newt, *Notophthalmus viridescens*, on one of their potential prey, tadpoles of the widespread frog *Bufo americanus*. Here the interesting pattern was that the predator subspecies that regularly occurred with *Bufo* had a much stronger per capita impact on prey than the one that did not. I suspect that there are many other examples of this sort of intercommunity variation in interaction strength that are correlated with differences in community structure. Reference to the range maps in a field guide to North American amphibians (Conant and Collins 1991) shows that there are many widespread species that potentially interact with very different numbers of less widely distributed species along well-known latitudinal gradients of species richness (Currie 1991). For example, populations of the widely distributed small frog *Pseudacris crucifer* interact with perhaps one or two anuran species in the northern parts of their range, and 10 times that number of anuran species in southern portions of their range. Whether populations from different parts of the geographic range will differ in competitive ability or in resistance to predators (see Morin 1983) is a fascinating question that begs to be answered.

There are other examples of geographic variation in community-level interactions. Thompson and Cunningham (2002) have described extensive geographic variation in coevolving plant-insect interactions, much of which has a clear genetic component. Paine (1980) also describes a situation in which the predatory sea star *Pisaster ochraceous* acts as a keystone predator in some parts of its range, whereas in other locations it appears to have no exceptional impacts on the community. Whether these differences reflect important genetic differences in the predator populations, differences in food web topology, or purely ecological processes driven by settlement rates (e.g., Gaines and Roughgarden 1985) remains unresolved.

A second issue concerns the extent to which coevolutionary changes alter the way in which species assemble into communities. Models have addressed whether communities will have fundamentally different compositions depending on whether they assemble from species with essentially fixed properties (no genetic change) or from species that coevolve during the process of assembly (Rummel and Roughgarden 1983). Interestingly, model communities with coevolving colonists support fewer species than systems assembled from species with fixed interaction strengths. The coevolving communities also show temporal turnover in species that is consistent with the taxon cycles described for ants and birds on island communities (Wilson 1961, Ricklefs and Cox 1972). Although a simple model of exploitative competition predicts that evolutionary changes will support less diversity than a

community assembled from non-evolving species, more complex evolutionary frameworks can lead to the promotion of extensive diversity through networks of intransitive competitive interactions.

One system in which community genetics may interact with species composition to actually maintain high levels of diversity is the microbial communities of soils (Czárán et al. 2002). Soil systems exhibit spectacular levels of microbial diversity that have been difficult to explain via traditional approaches, such as differences in resource utilization (e.g., Tilman 1982). However, if soil bacteria interact via nontransitive, competitive networks of the sort envisioned by Czárán et al. (2002) and Kerr et al. (2002), then there may be a major role for community genetics in maintaining diversity in natural communities. In these microbial systems, the evolutionary dynamics of genes coding for interspecific toxin production, resistance, and susceptibility drive the spatial distribution of diversity. In turn, both diversity and the genetics of keystone species can have important effects on ecosystem functioning, as pointed out by Whitham et al. (2003).

SOME CAVEATS

Some of the examples given by Neuhauser et al. (2003) and Whitham et al. (2003) focus on relatively low-diversity temperate systems in either natural or agricultural settings. It is interesting to ask whether similar kinds of processes might operate in much more diverse systems, especially if species in those systems interact with a greater diversity of selective agents. Novotny et al. (2002) suggest that the rarity and low density of individual tree species in tropical forests leads to the evolution of an insect fauna that is far more generalized than the assemblage that one typically sees in temperate communities. If this is a general pattern, the basic premise of community genetics described by Neuhauser et al. (2003) and Whitham et al. (2003) may not generalize well beyond low-diversity temperate systems, where strong species-specific interactions prevail.

Whitham et al. (2003) are correct in pointing out that genetic variation in keystone species can have major implications for community structure and ecosystem functioning. It makes good sense to extend traditional population genetics to include the more complex interactions among species that doubtless occur in communities. However, it is important not to conflate this useful framework with the far more controversial and problematic issue of selection acting on communities or higher levels of ecological organization. It is worth pointing out that, with few known exceptions (e.g., Currie et al. 1999), neither communities nor their dominant multispecies modules reproduce, disperse, or die as units. Instead, communities seem to assemble according to the individual properties of their component species (e.g., Davis 1981). This makes it difficult to imagine situations in which entire communities or their

even their component modules are the units of natural selection. For that reason, it seems prudent to avoid terminology that even indirectly implies that natural selection operates on entire communities. Consequently, I suggest avoiding the use of the terms “extended phenotypes” and “community heritability.” Both ideas can be readily expressed instead as consequences of natural selection acting on individuals. Unfortunately, these terms recall some of the discredited ideas of Frederick Clements (1916), who likened the development of natural communities to that of a superorganism. There are enough fascinating consequences of natural selection operating on individuals in the larger context of communities that community-level selection need not be invoked as an explanation.

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COMMUNITY GENETICS: TOWARD A SYNTHESIS

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INTRODUCTION

Community genetics, as initiated by Collins and Antonovics (Antonovics 1992), and elaborated on in the papers of this special feature (Neuhauser et al. 2003, Whitham et al. 2003), seems to be the critical missing

piece linking genetics and evolutionary biology with ecology. Both Whitham et al. (2003) and Neuhauser et al. (2003) present a series of stories showing how the genetic diversity of a species can influence other members of the community (and sometimes ecosystem properties), and how interacting species affect genetic diversity and natural selection of a focal species. They have not, however, provided a compelling argument that the community genetics perspective is fundamentally different from the current emphasis of much of

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evolutionary ecology, nor have they provided the necessary framework for ecologists to use the community genetics perspective within a synthetic approach to questions involving many interacting species.

In this response, we first ask how community genetics advances our understanding of fundamental ecological questions, as well as more applied issues regarding the conservation of rare species, and responses of species and communities to environmental change. We then discuss reasons why empirical studies of selection in response to interspecific interactions often do not connect with the theoretical studies on community genetics. Lastly, we suggest how empiricists can better link their current research programs to theoretical studies on community genetics.

What does understanding community genetics do for community ecology?

Over the past few decades, a majority of community ecology studies have become highly reductionistic, and experiments focus primarily at the fine detail of species interactions at local spatial scales. From this, many community ecology studies have become mired in the complexity and intricacies of this detail, and have greatly lost the ability to provide any sort of generalities (e.g., Lawton 1999, 2000). Community genetics takes us one more step down the reductionistic ladder, by adding genetic variation into the already complex picture. When do we need to go down this extra step?

Empiricists interested in broader questions of species diversity, distribution, and abundance will not be easily convinced that studying the genetic variation within species is important to their research program. At community and ecosystem levels of study, it is often difficult enough to keep track of different species, much less different genotypes within species. Consider an analogous type of reductionism: intraspecific stage (or size, age) structure. It has been convincingly shown by many authors that intraspecific variation in the stage of an organism can have dramatic effects on the structure of a community (e.g., Werner and Gilliam 1984). For example, when prey species are vulnerable to predators as juveniles, but invulnerable as adults, the nature of the entire food web can be very different than when prey are consistently vulnerable to predators (e.g., Chase 1999). In these sorts of cases, then, considering the complexity of stage structure can provide a much clearer understanding of the nature of interspecific interactions, as well as larger scale questions on the distribution and abundance of organisms. However, this does not mean that all species in a community should be classified by stage or size, or that studies that ignore stage structure are not adequate. The species within a community that are best classified by stage are obvious if one is looking for this. For example, species with complex life cycles, such as those with aquatic juvenile and terrestrial adult stages (e.g., frogs and many in-

sects), will interact with completely different species at different stages in their life cycle.

When a species has a large amount of genotypic variation in traits that play a strong role in interspecific interactions, then the community genetics approach, and the classification of organisms by genotype rather than by species, may be warranted. However, such guidance is not evident in the papers by Neuhaser et al. (2003) and Whitham et al. (2003). For example, Whitham et al. (2003) suggest that ecologists should focus on measuring the genotypic variation in species with disproportionate effects on the community/ecosystem (i.e., keystone species). We would instead argue that it is only necessary to measure genotypic variation in keystone species when that variation directly affects its traits that are known, or suspected, to influence the community/ecosystem. That is, the trick is for the empiricist to identify those species within a community for which further classification of organisms into genotypes would provide a better understanding of the abundance and distribution of other species in the community.

If the changes in the genetic structure of dominant or keystone species in the community have the potential to affect the persistence of other interacting species (as suggested by Whitham et al. [2003]), then conservation efforts may need to be shifted. Specifically, conservation genetics is almost exclusively studied at the population level, and focuses on the genetic variation of rare species and questions involving inbreeding depression and loss of heterozygosity (Amos and Balmford 2001). Such rare species are not likely to be keystone species within a community. Because species do not occur in isolation, conservation of species may be best addressed at the community level. When the conservation goals are at community and ecosystem levels, instead of at the population level, perhaps conservation geneticists should shift their focus to more dominant species, as suggested by Whitham et al. (2003).

The mismatch between theoretical and empirical work

One of the best ways for community genetics to achieve a synthetic framework is to develop a more intimate connection between theoretical and empirical research. However, there is a current mismatch between the theoretical work on community genetics (e.g., the models described in Neuhaser et al. 2003), which explicitly considers the numerical responses of interacting species, and much of contemporary empirical work, which often controls the density of one of the interacting species as part of an experimental treatment. Experiments with biotic agents of selection are often conducted in a manner similar to those with an abiotic agent. However, mortality imposed by abiotic factors represents a constant selective agent, whereas the mortality imposed by biotic factors will be a function of the density of the interactor. In some circumstances,

numerical responses of biotic selective agents can be ignored. For example, Antonovics (1992) recognized that the numerical responses of pathogens affecting a target crop species were of little importance to the system because the crop population density and genetic structure were reset every year. However, for most ecological questions, the density responses of the interacting species will play an important selective role.

As an example of the importance of numerical responses of the interacting species, consider studies on the evolution of plant tolerance to herbivory. These studies often manipulate the density of herbivores in a controlled experiment or simulate different levels of herbivory by clipping plants, and measure a response variable such as individual fitness. Of the nine selection studies cited in a recent review on the evolution of tolerance (Stowe et al. 2000), eight used either simulated herbivory or manipulated herbivory in a highly controlled manner, whereas only one employed relatively natural field conditions in which numerical responses of at least some herbivores were possible. Allowing herbivore densities to respond in selection experiments could cause very different results from those in which herbivore damage is kept constant. For example, a theoretical study by Chase et al. (2000) showed that the expected favored plant genotype was mediated by the density response of the herbivore. A more tolerant plant genotype actually increases the density of herbivores, which can then have stronger effects on a less tolerant genotype (see also Tiffin 2000). Thus, empirical studies that eliminate the ability of herbivores to respond, even when the plant is the ultimate response variable, will reach a very different conclusion about the predicted outcomes of selection on that plant species. Furthermore, these studies also ignore the numerical responses of the plants, and therefore show little about the effects of herbivory on lifetime fitness or population dynamics.

As another example, Day et al. (2002) showed, theoretically, that when a predator is allowed to respond numerically to changes in the density of its prey, the selective pressure that it exerts and the optimal life-history phenotype of the prey are very different than when the predator is not allowed to respond numerically. A majority of empirical studies that explore the selective consequences of predators on prey phenotypes eliminate predator numerical responses in the context of a community food web. These include many of the better known studies of aquatic predator-prey systems, such as phantom midges and zooplankton, dragonfly larvae and larval frogs, and crayfish and snails. In all cases, the predators, and sometimes the prey, were not allowed to show numerical responses to the treatments. Thus, the conclusions of the experiments may be very different than the predictions of

theory, as well as the actual selective pressures in nature.

How can empirical work be better linked with theoretical predictions? Although we argue that the majority of empirical studies in evolutionary ecology are limited because they do not allow for numerical responses, we do not wish to suggest that the only solutions are: (1) long-term experiments which encompass many generations, or (2) small-scale experiments on species with rapid generation times in microcosms. There is another way, but one that will require a step away from the traditional hypothetico-deductive experimental approach. For example, by combining short-term experiments on key aspects of the interactions (e.g., the functional response), observations of natural systems (e.g., demographic rates), and explicit simulation models, much more realistic empirical estimates of how a species responds evolutionarily to selective pressures imposed by interspecific interactions can be gained.

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COMMUNITY GENETICS AND SPECIES INTERACTIONS

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INTRODUCTION

Whitham et al. (2003) and Neuhauser et al. (2003) advocate the “marriage of ecology and genetics” into a new field of community genetics, but do so in different ways. Whitham et al. (2003) emphasize the community-shaping effect of genetic variation in keystone species, connected ecologically to other community members, whereas Neuhauser et al. (2003) emphasize strong selection in nonequilibrium, genetically subdivided communities. Both papers present compelling evidence from different systems to illustrate that genetic variation has detectable effects on species interactions and the composition of ecological communities. The genetically variable keystone species range from aspens to microbial pathogens and the community consequences can occur at trophic levels other than that of the focal species. With “community epistasis” (Whitham et al. 2003), a QTL (Quantitative Trait Locus) of a keystone species may affect the phenotypes of other species in the community with which the keystone interacts. Indeed, these kinds of community-level effects, if as common as Whitham et al. (2003) argue, will require the study of QTLs in a much broader natural context than is typically considered in molecular evolutionary genetic studies, whose “gene for” results are often viewed as independent of context.

Whitham et al. (2003) extend the minimum viable population size (MVP) in conservation genetics to the community level as “the minimum viable interacting population” (MVIP). This requires preserving keystone genetic diversity (even specific genotypes). They also advocate determining whether global ecological changes might be amplified by genetic interactions between species. Like Neuhauser et al. (2003), they are concerned with genetic subdivision and apply concepts from multilevel selection theory like “community heritability” and “community epistasis.” Do the examples presented constitute the foundation of a new field of “community genetics,” or do they emphasize the need to reintroduce genetics into community ecology?

RECIPROCAL GENETIC EFFECTS WITHIN EVOLVING COMMUNITIES

With gene interaction (epistasis) and genotype-by-environment interaction ($G \times E$), the context of gene

expression determines genotype fitness (cf., Schlichting and Pigliucci 1998). Clearly, context extends beyond the individual to include conspecifics, e.g., in kin selection (Wade 1980a), and the surrounding ecological community (cf. examples in Whitham et al. 2003). With $G \times E$ in metapopulations, different demes can experience different contexts, environmental and/or genetic, so that evolution can occur at different rates or different directions in each local deme (Goodnight 2000, Wade 2001, 2002). As a result, $G \times E$ and epistasis are fundamental to speciation and the origins of biodiversity (Wade 2002). Whenever the environment itself contains genes, as in ecological communities, context itself can evolve (Wolf et al. 2003). The standard conceptual framework, which assumes not only weak selection (as per Neuhauser et al. 2003), but also contextual variation independent of genetic change in an evolving species, must be altered. This is the foundation of Thompson’s (1994) geographic mosaic hypothesis, in which ecological communities are integrated by the reciprocal coevolution of their member species. The evolution of an allele depends not only on the context that it experiences, but also on the evolutionary trajectory of that context, i.e., the ecological community.

COEVOLUTION IN SINGLE COMMUNITIES

If the two species mix and interact randomly with one another, the strength and direction of selection on one species is dependent upon the mean value of the context provided by the other species. Keister et al. (1984) modeled this kind of within-community reciprocal coevolution and noted that: (1) coevolution takes place *between traits* in two species and not, strictly speaking, *between species*; and (2) the random diversification of coevolving characters depends on the *smaller* of the two effective population sizes. The MVP for a particular species may not be its own size but rather the smaller effective size(s) of its ecological partners. Differently put, if a keystone species is large but numerically rare, then its effective size is critical not only for maintaining the keystone itself, but also for maintaining coevolving traits in the myriad of other species with which it interacts. This is a more specific, theoretical rationale for the MVIP proposed by Whitham et al. (2003).

Neuhauser et al. (2003) call into question the “time scale argument” that has served as a barrier between

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Ecology and Evolution for decades. The relatively faster pace of ecological processes has justified treating species' members as equivalent, genetic constants; reciprocally, the Darwinian gradualism of evolutionary processes has justified the absence of ecology in genetic models. With strong selection and nonequilibrium dynamics, the disciplinary barrier becomes as conceptually permeable as it was in the 1970s. In single-species life-history theory (Charlesworth 1994), demographic equilibrium cannot be achieved without genetic equilibrium and vice versa. *One of the major goals of community genetics theory should be to determine whether this principle extends to the community.* If so, the marriage of Ecology and Evolution will be enduring.

COEVOLUTION IN METACOMMUNITIES

Coevolution today relies primarily on the comparative taxonomy of species interactions (e.g., Clark et al. 1992, Thompson 1994), in which correspondence between the phylogenies of interacting species, frequently hosts and endosymbionts, is the mark of genetic coevolution. Whitham et al. (2003), Neuhauser et al. (2003), and Thompson (1994) before them, however, consider the genetics of subdivided or "meta" communities. In a meta-community, "community heritability" has been defined as the among-community fraction of the genetic variance affecting coevolving traits (Goodnight and Craig 1996). The only existing empirical estimate of community heritability comes from the Goodnight and Craig (1996) study of competitive ability in meta-communities of the flour beetles *Tribolium castaneum* and *T. confusum*. They specifically contrasted population subdivision for each species alone (e.g., Wade 1980b) with community subdivision, i.e., both species coexisting together, and found community heritability for competitive outcome (identity of the winning species) and for time to extinction of the losing species. This study supports the claim of Whitham et al. (2003) that multilevel selection within species should be extended to entire ecological communities, a qualitatively different concept from noting that keystone species' genetic diversity affects the wider community.

Interestingly, Goodnight and Craig (1996) did not find any change in mean competitive outcome arising from association; the "community genetics" was evident only in the variance among communities and not in the average two-species interaction. Within communities, each species experiences the average effect of its competitor as environmental variation. Across a meta-community, however, variation experienced as environmental within a deme becomes heritable at the community level (Goodnight 1991), where among-community selection could serve to integrate community function.

For interacting species X and Y , with mean phenotypes Z_X and Z_Y , respectively, mediating the ecological

interaction, imagine that individual fitness is determined primarily by interaction with the other species. Let an individual of X with phenotypic value, z_X , have fitness, $w(z_X)$, equal to $(a_1 z_X + \alpha_{XY} z_X z_Y)$. The first term, $a_1 z_X$, is fitness independent of species Y (which I set equal to zero to emphasize interaction) and the coefficient, α_{XY} , captures the interaction effect. The traits might be corolla length and tongue length in the coevolution of a plant and a pollinating bee, for example. The selection differential on z_X in X is:

$$\begin{aligned} S(z_X) &= \text{cov}(z_X, w[z_X]) \\ &= (\alpha_{XY})(Z_Y)(V_X) + (\alpha_{XY})(Z_X)(G_{z_X Z_Y}) \quad (1) \end{aligned}$$

where V_X , is the variance of z_X among individuals, and G is the covariance of z_X and Z_Y . Context-specific fitness is evident in $S(z_X)$: (1) $(\alpha_{XY})(Z_Y)(V_X)$ shows that selection on z_X depends upon the average local context, Z_Y , provided by species Y (Keister et al. 1984, Wolf et al. 2003); and (2) $(\alpha_{XY})(Z_X)(G_{z_X Z_Y})$ shows that, if mean local context, Z_Y , covaries with trait, z_X , across communities, it also affects selection. Clearly, the fitness function for species Y might depend upon Z_X and G in different, and possibly opposing, ways. The covariance, $G_{z_X Z_Y}$, may evolve if X individuals vary in how they experience the presence of species Y . If $G_{z_X Z_Y}$ is zero before selection, it may be positive or negative after selection. That is, some X individuals will experience a relatively poor interaction with species Y and, consequently, will have low fitness, whereas others will have a favorable, fitness-enhancing interaction. For example, a nonzero $G_{z_X Z_Y}$ could occur from a nonrandom distribution of herbivores (species X with tolerance for secondary compounds, z_X) among host plants (species Y with concentration of secondary compounds, z_Y). (See also Carroll and Boyd [1992] for beak length and host plant type in soapberry bugs.) Overall, because mean fitness of species X increases when z_X and Z_Y *adaptively* covary, any feature of the community ecology that enhances the between-generation transmission of a positive association, $G_{z_X Z_Y}$, is favored by selection. Note that selection only in species X might result in a covariance, $G_{z_X Z_Y}$, with negative evolutionary consequences for species Y . By analogy with linkage disequilibrium in evolutionary genetic theory, selection creates "community disequilibrium" between genes in X with those in Y , which has an among-communities component. "Tightly coevolved" may mean reciprocal, positive values of G , but negative values (like predator-prey arms races; Geffeney et al. [2002]) may be more important to maintaining species diversity across a meta-community. However, pairwise species interactions can change sign with the addition of a third species (cf. Whitham et al. 2003), making prediction much more complicated and empirical estimation essential.

Random dispersal of either species diminishes community disequilibrium, whereas nonrandom dispersal maintains it, similar to the among-deme component of

linkage disequilibrium (Wade and Goodnight 1991, 1998). The comparative taxonomic approach misses this important aspect of the evolutionary dynamic, whereas the geographic mosaic hypothesis (Thompson 1994) is founded on it. By focusing at the species level, the comparative studies account for adaptation between species, but not the underlying coevolutionary dynamic that causes it. *The origin and maintenance of heritable covariation between two or more ecologically interacting species, i.e., community disequilibria, in response to community subdivision and within- and among-community selection is a critical theoretical and empirical task for community genetics.*

As per Whitham et al. (2003) and Neuhauser et al. (2003), a large number of ecological processes, especially those involving keystone species, affect the within-community mean fitness of many species. Thus, if the genotype of a keystone species varies among local communities, it would result in locally variable evolution across the meta-community and, consequently, in a geographic mosaic of character states in many other species. Thus, significant subdivision of one species may create the necessary genetic covariance across species that makes “community genetics” a novel and important area of study. Some of the empirical methods for estimating community heritability and community disequilibrium can be found in the multilevel selection studies of metapopulations (e.g., Wade 1980a, Wade and McCauley 1980, Goodnight 1991, Goodnight and Craig 1996, Wade and Griesemer 1998).

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COMMUNITY GENETICS AND COMMUNITY SELECTION

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These two papers under discussion (Neuhauser et al. 2003, Whitham et al. 2003) use James Collins' term "community genetics" (Antonovics 1992) to cover a diversity of topics, some new, some old, but worth revisiting or with a new twist. We will attempt to identify the major themes and add yet another important meaning to the idea of "community genetics."

The focus of Neuhauser et al. (2003) is to show that genetic evolution is a rapid process that takes place on ecological time scales, especially in non-equilibrium systems. Moreover, genetic evolution in a single species can be highly influenced by other species in the community, which means that population genetics and community ecology must be studied in conjunction with each other. The effects of species interactions on intraspecific evolution are sufficiently complex that they can result in a mosaic of outcomes over space. Although these points are relevant to evolution in all communities, some of the best examples come from human-influenced communities, which tend to be highly non-equilibrium.

The main point of Whitham et al. (2003) is to show that single species are genetically diverse, with important consequences for community and ecosystem processes. The emphasis is not on rapid evolutionary change, as in Neuhauser et al. (2003), but on genetic diversity that is maintained over time in a rough equilibrium. The message is that community and ecosystem ecologists frequently assume that species are homogeneous units and that ecological diversity exists only between species. Once we appreciate that ecological diversity also exists within species, the need to combine population genetics, community ecology, and ecosystem ecology becomes apparent.

As invoked by Whitham et al. (2003), the concept of an "extended phenotype" is similar, if not identical to, the concept of indirect effects that has already been emphasized as important in community ecology (Wootton 1994, Miller and Travis 1996). The example of the parasitic relationship between mistletoe and junipers made mutualistic by the inclusion of seed-dispersing birds, and the general conclusion that "scaling up stud-

ies to include one more species or environmental condition may reverse our basic conclusion" are statements about indirect effects that remain applicable even if the species are genetically uniform. Similarly, the consequences of indirect effects on ecosystem processes are important in their own right, even if species are genetically uniform. The novelty and appropriateness of the term "community genetics" lies not in making these points, but in showing that different individuals of the same species can produce very different indirect effects, with important consequences for community composition and ecosystem processes.

Although it is worth distinguishing the differences between these two articles, they do share the overarching theme that intraspecific and interspecific processes cannot be studied in isolation, as they have been so often in the past. With apologies for making an already complex subject even more complex, we now identify a very different concept of community genetics that, curiously enough, can take place without any genetic changes within species.

Consider an artificial selection experiment in which a population of individuals is measured for a trait such as body size, and one end of the phenotypic distribution is selected to create an offspring generation. If the phenotypic distribution of the offspring shifts in the direction of selection, there is a response to selection and the trait is partially heritable. Presumably, the response to selection is caused by a change in gene frequencies, and genetic evolution has taken place.

Now, consider a similar experiment in which the units of selection are groups rather than individuals. For example, Wade (1976) created groups of flour beetles, measured them after 37 d for the trait "group size," and selected one end of the phenotypic distribution to create a new generation of groups. The phenotypic distribution of the offspring generation shifted in the direction of selection, demonstrating that the group-level trait "group size" is partially heritable and responds to group-level selection. Again, the response to group selection presumably is caused by a change in gene frequencies, and genetic evolution has taken place. A number of artificial group-selection experiments have been performed (reviewed by Goodnight and Stevens 1997), and a group-selected strain of chicken has even been developed that lays more eggs and exhibits less aggression than individually selected strains (Muir 1995).

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Finally, consider an experiment in which the units of selection are multispecies communities rather than single-species groups. For example, Swenson et al. (2000*b*) created soil and aquatic microcosms inoculated with naturally occurring communities of microbes, measured them after a period of time for plant biomass (in the soil microcosms) and pH (in the aquatic microcosms), and selected from one end of the phenotypic distribution to inoculate a new set of microcosms. The phenotypic distribution of the offspring “generations” shifted in the direction of selection, demonstrating that ecosystem traits such as plant biomass production and freshwater pH can respond to community-level selection. Just as group-level selection can be used for practical purposes such as increasing egg productivity in chickens, community-level selection can be used for practical purposes such as developing microbial ecosystems that degrade toxic compounds (Swenson et al. 2000*a*).

Before addressing the question of whether community-level selection occurs in nature, let's examine the response to selection in the laboratory experiments. In the case of individual-level and group-level selection, evolution at the phenotypic level is caused by a change in gene frequencies. In the case of community-level selection, evolution at the phenotypic level could be caused by genetic changes in the component species, changes in the species composition of the community, or both. Goodnight (1990*a, b*) provides an example of community-level selection resulting in genetic changes in the component species. He selected a two-species flour beetle community for a number of traits, including density of one of the species. There was a response to selection and the proximate mechanisms included genes in both species that interacted with each other to influence the community-level phenotypic trait. In our experiments, consider the hypothetical case in which the original microcosms start with a very large pool of microbial species and the response to selection is accomplished entirely by changing the frequencies of the species without changing the frequencies of genes within species. Evolution has taken place, the communities have become “designed” by selection to produce the selected phenotype, and the response to selection has been caused by a change in the composition of the community. It seems like a trivial detail that the compositional change was in the proportions of species rather than the proportions of genes within species. Note also that changes in species composition or population sizes within an ecosystem literally constitute changes in gene frequency at the community level.

This reasoning suggests that the concept of “community genetics” (or ecosystem genetics, insofar as communities are selected on the basis of their ecosystem processes, as in our experiments) should be expanded in certain contexts to include all changes in the composition of the community, between and within

species. When selection acts at the level of whole communities, the community becomes analogous to an organism and the constituents of the community become analogous to genes within the organism. Populations of different species become roughly analogous to organs and chromosomes, interacting with each other to produce the phenotypic properties that allow the whole community to survive the community-level selection process. These category shifts seem strange at first, but they follow directly from the concept of community-level selection and are nicely illustrated by artificial selection experiments, which can be conducted with equal ease at the individual, group, and community/ecosystem levels. The discussion by Whitham et al. (2003) of community-level selection, which they frame in terms of the statistical method of contextual analysis, makes the same points at a more abstract level.

Even though community-level selection has been demonstrated in the laboratory, it remains to show that it operates in nature, requiring the expanded view of community genetics that we have outlined. We have discussed this issue elsewhere (Wilson and Knollenberg 1987, Wilson 1992, 1997, Swenson et al. 2000*a, b*) and must be content to merely raise it here, alongside the other meanings of the term “community genetics” discussed in the target articles.

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GENETICS, EVOLUTION, AND ECOLOGICAL COMMUNITIES

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Although “community genetics” will probably stay with us, some aspects of the usage of the term in this Special Feature trouble me. The papers by Neuhauser et al. (2003) and Whitham et al. (2003) do not make such a strong case for creating a new discipline or subdiscipline as they do for identifying important issues at the interface of ecology and evolution. Antonovics (1992) originally defined community genetics as “the study of genetics of species interactions and their ecological and evolutionary consequences [p. 448].” He felt that the term was needed to free ecologists from “the overly restrictive frame of reference, the reciprocity, that coevolutionists would chose for their own discipline [p. 429]” (e.g., Janzen 1980). As applied by Neuhauser et al. (2003), community genetics differs little from population and ecological genetics, and its use seems to diminish the relevance of an extensive, important body of work to contemporary issues in ecology. As community genetics is espoused by Whitham et al. (2003), it resurrects the apparently irrepressible idea of the community as superorganism (Clements 1936, Dunbar 1960), long ago rejected by most ecologists after decades of empirical study and argument (Gleason 1926, Whittaker 1965).

Both essays subscribe to the notion that strong selection of alternative genotypes in populations of “key-stone” species can have major impacts on ecosystem functioning. By definition, evolutionary response to selection increases the average fitness of the selected population. When the genetic makeup of a population responds to biotic interactions, the average fitness of competitor and consumer populations can decrease. The resulting demographic changes alter population in-

teractions and the various ecosystem functions associated with living organisms as regulators of community diversity and trophic structure, as energy transformers, and as nutrient cyclers. Thus presented, most ecologists would find the foundation of the community genetics idea to be sound. With the growing number of techniques for assessing genetic variation and evolutionary response in natural systems, most ecologists would also find the continued integration of ecological, genetic, and evolutionary perspectives completely natural and desirable.

This integration has a long history. Neuhauser et al. (2003) recognize that the roots of community genetics are nourished by the ecological genetics of E. B. Ford (1971) and Theodosius Dobzhansky (1951). This tradition was richly developed decades ago through studies such as those of Clarke and Sheppard (1960) on mimicry polymorphism, Owen (1963) on apostatic selection by predators, Mode (1958) on coevolutionary dynamics (coining the word “coevolution” nearly a decade before Ehrlich and Raven’s (1965) classic paper), or Pimentel (1968) on the genetics of competition and predation. Indeed, Antonovics (1992) suggested that community genetics should be considered a subdiscipline of ecological genetics.

The distinction that Neuhauser et al. (2003) make between ecological genetics and community genetics—that the new field deals with nonequilibrium systems and strong effects, whereas the old does not—is false. Neuhauser et al. state that “The community genetics framework provides new understanding when selection alters genetic composition on the same time scale as that on which numerical abundances change.” Thus, these authors associate community evolution with strong selection and rapid response, and they associate population genetics with weak selection and slow evolutionary responses. They use several recent examples of the evolution of resistance of populations to path-

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ogens to support this dichotomy, but they might as well have turned to some of the earliest examples of population and ecological genetics. Many of these involved strong selection and rapid evolutionary responses in non-equilibrium systems, e.g., cyanide resistance in scale insects (Quayle 1938, Dickson 1940) and industrial melanism (Kettlewell 1973), often in host–pathogen systems, e.g., sickle-cell trait (Allison 1956), myxomatosis (Fenner and Ratcliffe 1965), and wheat rust (Williams 1975). Clearly, anthropogenic changes in the environment can exert strong selection on populations and elicit rapid evolutionary responses that might have important consequences for communities and ecosystems (Palumbi 2001). Ecologists should pay close attention to these dynamics in the contexts of such issues as emerging disease, changing trophic structure of communities, and imbalances in the regulation of ecosystem function. This insight might have been ignored by some ecologists, but it is not new.

Whitham et al. (2003) take the idea of community genetics a step further by arguing that the cascading effects of individual traits through the ecosystem (the “extended phenotype”) create heritable community traits, which allow communities to respond to selection as a unit. Few data support communities being integrated entities with discrete boundaries (i.e., units of selection). Even cases of close mutualism, such as mimicry complexes and plant–pollinator relationships, break down as examples of tightly coupled coevolution (Pellmyr and Thompson 1992, Thompson 1994, Thompson and Cunningham 2002), leaving a small number of examples from obligate mutualisms and host–parasite interactions (Hafner et al. 1994, Moran and Baumann 1994, Page and Hafner 1996; but see Ricklefs and Fallon 2002). Indeed, Antonovic’s (1992) advocacy of “community genetics” appears to have been partly a reaction against this type of community thinking.

Evolution follows upon the existence of heritable variation in fitness. Even if communities did exist as discrete units, evolution of populations within communities would weaken the heritability of community traits (Lewontin 1970, Wilson 1976; but see Gould 1999, Johnson and Boerlijst 2002). Although strong interdependencies occur and undoubtedly guide evolution, and although genetically determined qualities influence the array of species with which an individual interacts, these “community” qualities can be understood and communicated by the conventional vocabulary of ecology, population genetics, and evolution. Terms such as “extended phenotype” and “community genetics” evoke a structure that scarcely exists in nature.

Although I have complained (perhaps even whined a bit) about “community genetics” and its associated terms as unnecessary and potentially misleading, I also share the belief of most ecologists in the integration of ecology and evolution. The studies described in the

papers by Neuhauser et al. and Whitham et al. represent important areas of overlap between these disciplines, involving genetic variation in consumer–resource relationships, especially defenses against herbivores and pathogens, that can influence the composition of species assemblages and ecosystem function. A number of related issues, which appear to me to be ripe for unification of ecology and genetics at the community level, exemplify the richness of this endeavor. In this regard, the papers in this special feature make an important point. Although the mechanisms of evolution might be studied most efficiently by extracting evolving systems to the laboratory or to models, evolution takes place in natural systems and has consequence not only for the gene pool and its phenotypic expression, but also for the systems themselves. The field of “evolutionary ecology” developed during the 1960s to provide adaptive interpretations for patterns in nature, primarily regarding life history and behavioral phenotypes of organisms (Williams 1966, Roff 2002). No coherent, parallel movement of “ecological evolution” arose to provide a natural context for understanding the results of evolution.

Four issues, beyond those raised by Whitham et al. (2003) and Neuhauser et al. (2003), that interest me in particular are (1) the evolution of abundance and range size, (2) maintenance of genetic variation for traits that have a strong influence on population properties and community function, (3) formation of new species, and (4) evolutionary assembly of ecological communities. Most of the variance in population density and range size resides at a low taxonomic level (Gaston 1998) and would appear to reflect microevolutionary changes in population interactions, associated, for example, with genetic variation in pathogen virulence and host resistance (Pimentel 1968, Ricklefs and Cox 1972, Van Valen 1973). Models of host–parasite interactions feature the stable maintenance of variation in resistance and virulence alleles with limit-cycle like dynamics in both population size and allele frequency with time constants on the order of tens of generations (May and Anderson 1979, Antonovics 1992: Fig. 18.6). The longer time scales of the dynamics of range expansion and contraction, on the order of 10^5 generations in Lesser Antillean birds (Ricklefs and Bermingham 1999, 2001), imply a potential role played by novel genetic variation through mutation. Understanding the dynamics of this process will require detailed genetic and ecological comparisons of closely related species with contrasting range sizes.

Both Neuhauser et al. (2003) and Whitham et al. (2003) emphasize the importance of genetic variation within populations, yet the maintenance of such variation, especially for traits potentially under strong selection, has been a long-standing problem (Lewontin 1974). Population geneticists believe that most variation is maintained by spatial variation in the environment and by frequency-dependent selection mediated

primarily by predators, pathogens, or social interactions within populations (Hartl and Clark 1997). How individuals are distributed across the environmental template that maintains genetic variation, and how the resulting pattern of genetic variation within a population evolves, requires close attention to the distribution of genetic variation against the ecological background (Thompson 1994).

Diversification of ecological roles within species assemblages, i.e., adaptive radiation (Givnish 1997, Losos et al. 1998, Schluter 2000), begins with the formation of new species. In some theories, the speciation process drives diversity (Hubbell 2001). Most models of speciation include ecological or geographic components, but the relative importance of external (geography, habitat, and interspecific interactions) and internal (genetic mechanisms and intraspecific interactions), including lineage-specific (Heard and Hauser 1995), factors is not understood (Howard and Berlocher 1998, Magurran and May 1999, Moritz et al. 2000). I suspect that progress will come as ecologists, population geneticists, and evolutionary biologists continue team efforts to study patterns of incipient species formation (Avisé and Walker 1998).

Finally, although field ecologists, recognizing the open structure of species assemblages, long ago abandoned the unitary concept of communities, assembly theory has been built largely on models of the invasion of discrete communities by "non-evolving" species drawn from external species pools (Morton et al. 1996). In reality, local assemblages are built up as species extend their distributions from other localities or adjacent habitats where the invaders are also established members of local assemblages. This process of extension (and also contraction and withdrawal of species from local assemblages) might involve evolutionary change in relationships with pathogens, food resources, or physical conditions in the environment, sometimes dramatically, as in the case of the invasion of mangrove environments by terrestrial lineages of plants (Hutchings and Saenger 1987, Ricklefs and Latham 1993). The coexistence of sister taxa formed by speciation, by which diversity may be increased locally, also involves the evolution of ecological divergence (Barraclough et al. 1999, Grant and Grant 2002). Until we synthesize the ecology and evolution of species formation, habitat shift, and establishment of secondary coexistence, it is unlikely that we will be able to interpret patterns of biodiversity in terms of the processes that produce them. I am very much in favor of injecting genetics and evolution into ecology, and vice versa, but we don't need a special term for this synthesis. Let's just get on with it!

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INTEGRATING MICRO- AND MACROEVOLUTIONARY PROCESSES IN COMMUNITY ECOLOGY

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INTRODUCTION

Neuhauser et al. (2003) and Whitham et al. (2003) clearly demonstrate the powerful insights that can be gained from examining the evolutionary process in an ecological context by combining community ecology and population genetics. These approaches show how organism interactions can influence rates and direction of evolution, and how genetic variation within populations can influence patterns of species abundance and diversity within communities. In doing so, they provide insights into microevolutionary processes in rapidly evolving organisms and demonstrate the far-reaching consequences of intraspecific genetic variation for community structure. This merging of ecology and genetics invites an even larger view, that of integrating both micro- and macroevolutionary processes in community ecology.

The incorporation of phylogenetic analysis in community ecology (e.g., Brooks and McLennan 1991, Ricklefs and Schluter 1993, Losos 1996, McPeck and Miller 1996; reviewed by Webb et al. 2002) has arisen parallel to the emergence of community genetics. Just as the development of quantitative and population genetic techniques for examining evolutionary change within populations has made community genetics possible, so has the development of modern phylogenetic and comparative methods allowed advances in phylogenetic community ecology. These parallel advances allow, for the first time, a synthetic ecological perspective that incorporates an understanding of both the micro- and macroevolutionary processes that influence community structure.

Ecological communities are assemblages of co-occurring species that potentially interact with one another. They are the result of not only present ecological processes, but also past and continuing evolutionary processes (McPeck and Miller 1996). Even the agricultural communities studied by Neuhauser et al. (2003) reflect the evolutionary history and continuing evolution of their constituent organisms. The genetic

and phenotypic outcomes of these evolutionary processes have far-reaching consequences for the ecological interactions of species, as illustrated in rich detail by Whitham et al. (2003) and Neuhauser et al. (2003). While community genetics allows examination of how present-day genetic variation influences community dynamics, incorporating a phylogenetic perspective into community ecology allows investigation of the historical processes that influence these dynamics. Phylogenetic information reveals the extent to which organisms have a shared evolutionary history, and it can help us to understand the genetic and phenotypic properties of species. It can also provide information about the relative timing of historical events. This broader perspective allows us to ask where the collection of species we see coexisting today comes from (Manos and Donoghue 2001), why these species have the phenotypic properties they possess (Schluter 2000), and why other types of species are not present (McPeck and Miller 1996). In this essay, we illustrate how phylogenetic information can be combined with community genetics to address several kinds of questions.

DISTINGUISHING ADAPTIVE EVOLUTION FROM LINEAGE SORTING

*How tightly interconnected are species within communities ("ecological locking," sensu Jablonski and Sepkoski [1996])? Are ecological characters in community assemblages the result of adaptive evolution, coevolution, or the sorting of preadapted lineages?—*Species living together in communities vary in the degree to which they influence one another. At one end of the spectrum, coexisting species may exert strong enough selection on each other that one species' impact may lead to speciation of the affected species even before postmating genetic isolating mechanisms are present in the second, affected species (Wade 2001). Whitham et al. (2003) describe, for example, how interactions between moths and different genotypes of pinyon pine with contrasting chemical composition reinforce the maintenance of genetic variation in pinyon pine. Through these interactions, apparently small genetic changes can lead to a cascade of plastic morphological changes (sensu West-Eberhard 1989) that affect other community members. This patchy selection for different genotypes may ultimately result in the spe-

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ciation of pinyon pine (see Sultan 1995), depending on the spatial distribution and strength of different selection pressures (McPeck 1996).

At the other end of the spectrum, species may simply be “co-present” (Bazzaz 1996), and while coexisting in a predictable fashion, they may not influence one another in an evolutionary or selective sense. Coevolution only occurs when species’ interactions result in reciprocal genetic change. Species that do not currently show a measurable influence on one another may nonetheless have done so in the past. Such historical interactions may be elucidated by a broader view that incorporates both an analysis of genetic variation within and among populations and phylogenetic and ecological information about related species in other communities (Losos et al. 1998).

Perhaps the most famous example of the importance of considering a phylogenetic perspective when interpreting species interactions across communities is that of the *Anolis* lizards in the Lesser Antilles (summarized in Losos 1996). Throughout the Lesser Antilles, wherever two species of *Anolis* lizards coexist on an island, there is one large and one small species; lizard species that live alone on islands are of intermediate size. Recent analyses have shown that this common pattern is actually the result of two different processes. In the northern islands, the large and small species appear to have evolved in situ and are the result of character displacement resulting from sympatric evolution. However, in the southern islands the large and small species have not experienced predictable directional selection following introduction. Instead, it appears that ecological sorting has occurred such that only species with significantly divergent morphologies were able to colonize successfully. In the absence of phylogenetic information, it would be impossible to distinguish between the two different causes for the same pattern.

Using a phylogenetic approach, Janz and Nylin (1998) reanalyzed Ehrlich and Raven’s (1964) classic hypothesis of stepwise escape and radiation between butterflies and their host plants. By incorporating phylogenetic and fossil evidence, they were able to show that butterfly diversification postdated the diversification of their plant hosts, making the hypothesis of reciprocal diversification unlikely. Their inclusion of the relative timing of diversification in phylogenetic analyses of these lineages enabled them to hypothesize that butterfly evolution is linked to colonization of new plant lineages rather than to cospeciation.

While community genetics approaches can reveal possible mechanisms by which organism interactions might lead to speciation and how genetic variation within species can influence community composition, phylogenetic approaches have the potential to discern the mechanisms by which past organism interactions or environmental changes have influenced current diversity or current community assemblages. Combined, the two approaches are likely to offer a more synthetic

view of community evolution and to increase our ability to predict the future of communities.

INTRINSIC FEATURES OF LINEAGES

What role do intrinsic and idiosyncratic features of lineages play in influencing diversity and other community features? Are some communities more diverse because they include lineages that are inherently more likely to diversify or are less vulnerable to extinction?—Potential to diversify and susceptibility to extinction might be related to intrinsic features, such as population structure (Losos 1996), plasticity (e.g., Sultan 1995, Schlichting, in press), or evolvability (Wagner and Altenberg 1996), or alternatively, to differences in the strengths of selection pressures in different populations resulting from differences in organism interactions in those populations (McPeck 1996).

Insights about such intrinsic features of lineages using phylogenetic approaches may inform studies of current evolutionary processes, such as those examined by Neuhauser et al. (2003). For example, in exploring rates of evolution of resistance of the European corn borer (*Ostrinia nubilalis*) to Bt corn, we might gain perspective by knowing something about rates of diversification in the corn borer lineage in comparison to rates in other butterfly lineages and in other corn pest lineages. Janz et al. (2001) observed that polyphagous butterfly lineages are more speciose than those that specialize for particular plant host lineages. This led them to postulate that expansion of insect ranges to other hosts, possibly through evolved resistance to new secondary compounds (e.g., Zangerl and Berenbaum 1993), may be linked to diversification. Information about whether the European corn borer and associated pests are found within polyphagous or specialized lineages may allow us to predict whether these organisms have the evolutionary potential to escalate resistance rapidly to a new toxin.

Similarly, phylogenetic information could reveal whether corn smut (*Ustilago maydis*) shows potential for rapid evolution of increased virulence, based on previous diversification rates. How host specific is corn smut, and did it arise within a diverse lineage? In other words, is the evolutionary “cold spot” that Neuhauser et al. (2003) hypothesize characteristic of the lineage, or is this a unique pattern found only in relation to anthropogenic systems?

While community genetics emphasizes intraspecific genetic variation of interacting organisms, the phenotypic variation in traits of organisms in response to the environment (plasticity or polyphenism) is also likely to influence ecological and microevolutionary processes (e.g., Sultan 1995). Whitham et al. (2003) point out the importance of genotype \times environment interactions in their examples of the polyphenism in pinyon pine that results from moth attack and the decreased resistance of willows to herbivores after fertilization. There is a growing recognition that plasticity may be

Box 1. An illustration of how trait evolution can influence the phylogenetic structure of communities

A hypothetical scenario (shown in Fig. 1) illustrates the potential of phylogenetic analysis for understanding community assembly of three major community types (forests, swamps, savannas) present in a given geographic region (~100 km²). In the case of phylogenetic attraction (Fig. 1A, top left diagram), closely related species occur together, presumably because they share traits important for environmental filtering (Webb 2000). In the case of phylogenetic repulsion (top right), closely related species occur in different communities, possibly as a result of either current or past competition, so that individual communities contain distantly related species. Researchers can identify these patterns by examining correlations of phylogenetic distances between species pairs (using branch length distances) and their co-occurrence (how often they are found together in communities; Fig. 1A, bottom left and right panels).

These contrasting patterns of attraction and repulsion can be explained, in part, by an examination of the evolutionary convergence and conservatism of phenotypic traits (and habitat factors) among these species. The correlation between trait value similarity (or difference) and phylogenetic distance is one method for quantifying trait conservatism (Böhning-Gaese and Oberrath 1999; see also Ackerly and Donoghue 1998). Fig. 1B shows the correlation coefficients for the relationship between trait similarity and phylogenetic distance as well as between trait similarity and co-occurrence, in left and right panels, respectively, for several traits. In the left panel, those with a positive r value are convergent (labile); those with a negative r value are conserved. Data are nonparametric and null models are generally required for significance testing (see, e.g., Ackerly 1999). In the right panel, those traits that show a positive correlation with co-occurrence may be important for environmental filtering (phenotypic attraction; Webb et al. 2002), and those that show a negative correlation may be important for competitive exclusion or other processes that hinder co-occurrence (phenotypic repulsion; Webb et al. 2002).

Rooting depth of plants, which in this hypothetical example is conserved (Fig. 1B, left panel), may influence community structure and lead to phylogenetic repulsion by forcing species with similar rooting depth (closely related species) to occupy different habitats. Species with contrasting rooting depths (distantly related species) would be complementary and able to coexist (Parrish and Bazzaz 1976). Similarly, resistance to disease may also influence community structure. If disease resistance were highly conserved, as in the example presented here, then one could hypothesize that the co-occurrence of closely related species leads to increased density-dependent mortality (Janzen-Connell hypothesis [Janzen 1970, Connell 1971]) beyond the level of the species to higher phylogenetic levels. The interspersed of susceptible and nonsusceptible species (distantly related species) might decrease density-dependent mortality and thereby contribute to a pattern of phylogenetic repulsion.

In contrast, traits such as fire and desiccation tolerance which are convergent in this example (Fig. 1B, left panel), appear to be important for environmental filtering, because species that co-occur have similar trait values (right panel). Although trait conservatism may be the result of morphological or architectural constraints or the maintenance of ecological niches within lineages, these scenarios do not explain why closely related species have contrasting environmental tolerances, as suggested by the high level of convergence in desiccation and fire resistance, etc. Parallel adaptive radiation, in which character displacement causes differentiation and specialization for contrasting habitats and, ultimately, speciation across multiple lineages, could generate such a pattern. In "closed" systems, such as on undisturbed islands, where all species present are likely to have evolved together and all extant members of the lineage are present, this is a safe interpretation (for caveats, see Schluter [2000], Webb et al. [2002]). Most communities are likely to be a composite of species that have interacted over evolutionary time scales as well as newcomer species (Losos 1996). In these cases, it is important to have information about phenotypic traits of other members of the lineage not present in the regional species pool, and about whether these species have occurred together over evolutionary time scales. Fossil data can begin to provide evidence about which species have interacted in the past and for how long (Jablonski and Sepkoski 1996). These kinds of analyses should give us insight into the evolutionary processes and mechanisms involved in the assembly of communities and offer perspective on the current ecological dynamics and microevolutionary processes occurring within them.

positively linked to speciation and diversity of lineages (West-Eberhard 1989, Janz et al. 2001, Schlichting, *in press*), although the underlying mechanisms for this are unclear (see Agrawal 2001). Plasticity may lead to diversification of lineages through ecological means if species that exhibit high levels of plasticity are more likely to experience vicariance events due to their broad distribution. Alternately, the coincidence of plasticity and lineage diversity may be attributable to the ephemeral nature of highly specialized taxa, due to either intrinsic factors (high extinction rate) or to a trend toward niche expansion with lineage age (Kelley and Farrell 1998). Phylogenetic analyses that consider both the transition from generalist to specialist (such as those in Kelley and Farrell 1998) and the historical

distribution of species may help to distinguish between these causes. On the other hand, plasticity may provide an alternative to speciation, because plastic individuals can successfully colonize a wide range of habitat types, and genetic differentiation of populations or formation of ecotypes in different habitats may not be necessary (Sultan 1995, Sultan and Spencer 2002).

Both the tendency to diversify and susceptibility to extinction may play a role in one of the most spectacular radiations ever documented in the animal kingdom. Farrell (1998) explored diversification within two of the currently most speciose families in the world, the phytophagous weevils (Curculionidae) and leaf beetles (Chrysomelidae). Both families contain members that feed on both gymnosperms and angiosperms, and both

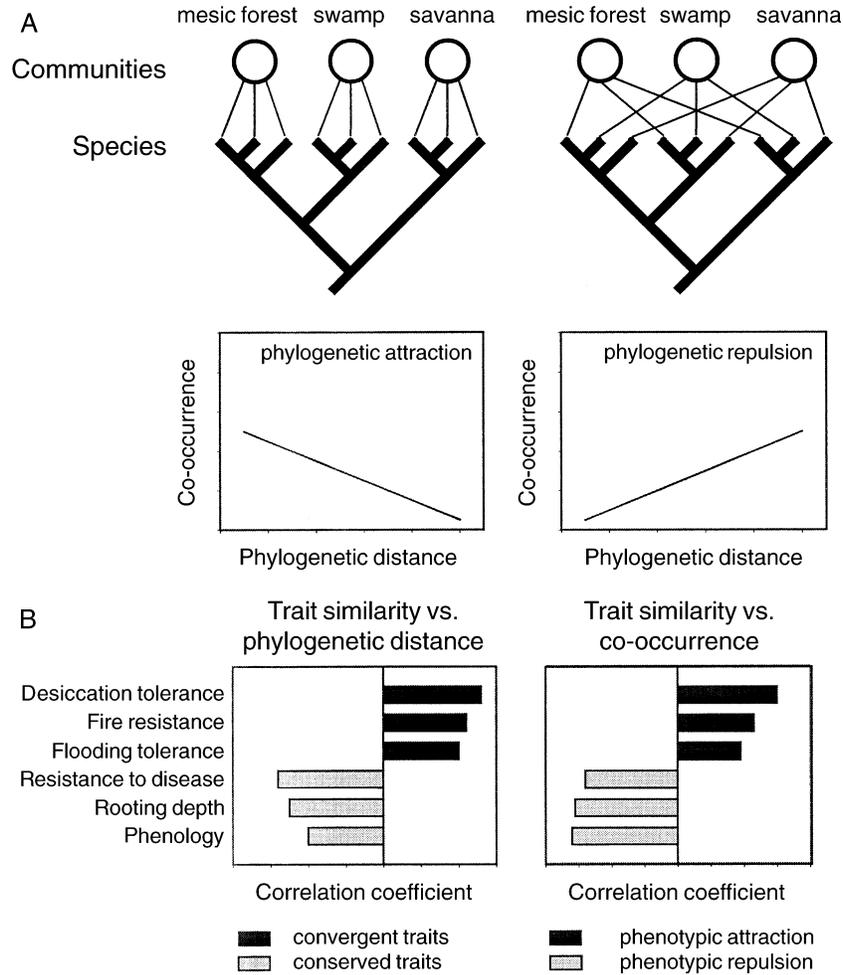


FIG. 1. (A) Alternative scenarios for the phylogenetic structure of communities. (B) Metrics to examine convergence and conservatism in trait evolution (left panel) and to identify traits that may be important in the assembly of communities (right panel).

families were in existence before the putative appearance and rise of angiosperms. Every group in each of these two families that switched from feeding on gymnosperms to angiosperms underwent a pronounced radiation. Angiosperms tend to be heavily preyed upon by herbivores, but they produce a great diversity of defensive compounds that may allow them to escape temporarily from their specialized herbivores. Given that beetles are markedly conservative in their associations (Farrell 1998), those beetle lineages that had historically fed on angiosperms were most likely to track their escaping hosts successfully and speciate in the process. Insect lineages show low extinction rates (Labandeira and Sepkoski 1993), and this may also contribute to the current extraordinary diversity of phytophagous beetles. Thus both ecological consequences of conserved phenotypes (preference for angiosperm hosts and host specificity) and intrinsic properties of beetle lineages (low extinction rates) have influenced

the current prevalence and distribution of phytophagous beetles in communities worldwide.

Neuhauser et al. (2003) examine the effects of fragmentation in Midwestern prairies on persistence of purple cone flower (*Echinacea angustifolia*) populations from two perspectives, which they distinguish as genetic (number of self-incompatibility alleles, rate of inbreeding) and ecological (dispersal of pollen and seeds, influence of fire). They suggest that coneflower can serve as a model species for many prairie natives because of shared life history characteristics. Although this may be true, distinct prairie lineages may have intrinsic properties with respect to inbreeding-related characters. Different taxa show different rates of evolution and maintenance of self-incompatibility alleles (Lawrence 2000); these differences can be related to the type of incompatibility mechanism (e.g., sporophytic vs. gametophytic), which is usually correlated with taxonomic affiliation. An examination of these

kinds of traits among the Asteraceae and other prairie lineages may illuminate not only lineage-specific parameters for the Neuhauser et al. model, but also the extent to which different species may be capable of evolution in response to changing population structure.

TRAIT EVOLUTION AND ASSEMBLY RULES IN STRUCTURING COMMUNITIES

Are there assembly rules in the structuring of communities that are linked to the evolutionary history of species? What insights into mechanisms that allow multiple species to coexist within a community arise from understanding trait evolution and the genetic underpinnings of trait expression?—The phenotypes of organisms determine how species interact and how they relate to their environment. Whitham et al. (2003) emphasize the importance of variation in phenotypes resulting from genetic variation within species and demonstrate that these phenotypic differences influence the way in which individuals of one species interact with individuals of other species. Although they clearly show that intraspecific genetic and phenotypic variation can impact community structure, variation across species may be more important for community dynamics. Moreover, if one of the central goals of community genetics is to understand community evolution, as Whitham et al. (2003) and Neuhauser et al. (2003) indicate, understanding past evolutionary processes at multiple phylogenetic scales is critical in providing a context for current evolutionary processes.

For example, knowledge about the phylogenetic structure of communities (Webb 2000) and the evolution of phenotypic traits of co-occurring organisms (and their relatives) can be used to determine (1) how convergent or conserved phenotypes are through evolutionary time (e.g., Ackerly and Donoghue 1998), and (2) how important environmental filtering vs. competitive interactions are in the assembly of communities (Weiher et al. 1998). Such macroevolutionary approaches may reveal patterns of phylogenetic attraction (Webb 2000) or repulsion (J. Cavender-Bares, D. D. Ackerly, D. Baum, and F. A. Bazzaz, *unpublished manuscript*) among members of a community (see Box 1 and Fig. 1). When combined with analyses of trait convergence and conservatism, such patterns can be used to generate hypotheses about mechanisms of coexistence (e.g., Wills et al. 1997) that can be tested using experimental and modeling approaches. Meanwhile, community genetics can provide insight into the current processes of niche differentiation and biotic interactions that facilitate coexistence.

In his pioneering study on the phylogenetic structure of rain forest communities in Borneo, Webb (2000) found that tree species that were closely related occurred together more often than expected (phylogenetic attraction). He hypothesized that the conservation of phenotypes within lineages caused phenotypically similar species to occur in similar habitats via environ-

mental filtering. In a related study on meadow communities in Great Britain, Silvertown et al. (2001) found that patterns of both attraction and repulsion emerged, but at different phylogenetic scales. At the broadest phylogenetic scale, eudicots and monocots were found to occupy the same niches less often than expected (phylogenetic attraction). Examination of phenotypic traits and their conservatism or convergence, as well as patterns of correlated trait evolution, can reveal whether environmental filtering is indeed a likely explanation for such a pattern, and which traits are critical for environmental filtering (Ackerly 1999). Are convergent traits the result of past competition and differentiation? With sufficient information about species within lineages and how long they have been together (see Webb et al. 2002), phylogenetic approaches to community ecology allow us to make inferences about the past evolutionary processes and traits that influence the sorting and assemblage of species. This information may improve our understanding of how diversity is maintained within communities.

Finally, we can try to examine why particular traits are conserved or convergent through evolution. There are a number of possibilities, including the hypothesis that traits that are controlled by fewer loci and are not closely linked to other traits (either by genetic linkage or pleiotropy) are likely to be less constrained and more evolutionarily labile (e.g., Etterson and Shaw 2001). In addition, the genetic structure of certain traits may have greater evolvability (Wagner and Altenberg 1996). Important trait loci have been identified for an increasing number of traits and taxa, as Whitham et al. point out, allowing the study of both genetic behavior and properties of traits, as well as their flexibility over macroevolutionary time scales. If links can be found between genetic structure, on the one hand (community genetics), and the long-term evolution of traits on the other (phylogenetic approaches), we can begin to provide microevolutionary explanations for macroevolutionary processes that have consequences for community assembly of organisms and organism interactions within communities. Such merging of community genetics and phylogenetic approaches in ecology is likely to bring new insights about how communities evolve and to allow us to predict where they are headed.

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TOWARD COMMUNITY GENOMICS?

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Having posited the idea that community genetics may be an important and rich area for scientific enquiry, I unfortunately couldn't find an excuse to decline the invitation to provide a commentary on the two papers featured in this issue of *Ecology* that use the concept of community genetics as a unifying theme! Perhaps in part reflecting some healthy skepticism on his part, the editor also asked me to comment on the issue of whether there is really anything novel and unifying in this idea and whether it really is useful! I should perhaps start with the latter issue.

All scientific disciplines have their own dynamics, including periods of decline and disillusionment. Questions that once were pressing have been answered, initially contentious dichotomies have wilted, and the importance of technical correctness starts to exceed the importance of the questions that can be feasibly addressed. Fortunately, however, most areas of science can still be refreshed and invigorated in exciting and often unpredictable ways. When the excitement comes about as a result of technical innovations (e.g., DNA sequencing, PCR, RNA interference), the directions and opportunities are often clear-cut and almost algorithmic. In ecology, a good example is the ready access to fast desktop computers that has fuelled a huge interest in seeing "what happens" when previous ecological models are made spatially explicit. Another example of a technical advance in ecology that opened up many new directions is the application of mass spectrometry to measure stable isotope ratios and to infer physiological processes at an ecosystem level. However, when the advance is conceptual, it is far harder to pinpoint where these new ideas are likely to lead, or to jump at obvious research directions: the issue is often reinterpretation of the known, rather than clear directions for new discovery. Additionally, conceptual shifts are nearly always heralded by an uncomfortable mix of reality, hype, and politics. They are also often instantiated by new words and phrases that can be likened to the flags or insignia of olden days. In those days, the chevron, cross, and castle were symbols whose syntactical content was sparse, but their new colors and combinations inspired conquests and

trumped previous incarnations of these selfsame symbols.

We have seen this mixture of reality and hype most overtly in the growth of molecular biology. I have always felt most sorry for "real" molecular biologists (who actually study protein folding and action at the molecular level) because they were so solidly trumped by these semantic fashions. Their only recourse seems to have been to resort to the old-fashioned sounding "structural biology" as a descriptor for their discipline, whereas most biochemists simply renamed themselves as "molecular biologists" and carried on in large measure as usual!

With regard to community genetics, we can certainly question whether there is anything new in the idea that deserves its own flag. The issues that are raised in these two featured papers (Neuhauser et al. 2003, Whitham et al. 2003) have been discussed sporadically for many years and in many ways. For example, at the start of my graduate courses over the past 25 yr, I have handed out the Ecological Geneticist's Creed (Table 1) as a somewhat tongue-in-cheek, but hopefully provocative statement of the challenges of combining ecological and genetic worldviews (see also Antonovics 1976, Enderler 1991, Lenski 2001). Indeed, the second tenet of the creed directly addresses genetics and community ecology.

So do we need a new name or a new discipline of community genetics? Certainly we hope that job descriptions will follow! I think "whether we need it or not" is the wrong question. The correct question is whether it will be accepted or not, and become established in the sociopolitical context of our discipline. The use of the term will be dictated less by whether the label is accurate, new, or apposite (remember the structural biologists), but more by whether it is useful. Already there have been some very tangible successes. For example, at the University of Minnesota, the Minnesota Center for Community Genetics founded in 1994 has integrated applied and pure scientists interested in species interactions at many levels (e.g., plant–insect interactions, crop–pathogen interactions, weed communities) and has received support from both the U.S. Department of Agriculture and the National Science Foundation. In this context, it is very relevant that both of the featured papers point out that their observations and results have direct relevance for applied biology. I was particularly struck by the point that ge-

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TABLE 1. The ecological geneticist's creed.

Creed	Explanation
Explaining the abundance and distribution of organisms is a genetic problem.	The ecological amplitude of a species both within and among communities has a genetic component.
The forces maintaining species diversity and genetic diversity are similar.	An understanding of community structure will come from considering how these kinds of diversity interact.
Adaptation is a dynamic process, operationally definable, and not just an emotional matching of the character to the environment.	Fitness and the contribution of phenotypes to fitness can be measured in terms of the mortality and fecundity of individuals within populations.
Environmental change will be accompanied by changes in both genetic composition and changes in numerical dynamics.	Genetic response is likely to result in compensatory changes in fitness and life-history components.
The distinction between "ecological time" and "evolutionary time" is artificial and misleading.	Changes of both kinds may be on any time scale: in principle, evolutionary and ecological changes are simultaneous.
The genetic quality of offspring is as important as the quantity.	Sexual systems are concerned with regulating the genetic quality of offspring.
The view that there is always an "evolutionary play" within an "ecological theater" is artificial and misleading.	The "ecological play" often happens in the "evolutionary theater." Selection at the genic or cellular levels may have phenotypic effects with enormous ecological consequences. Genetic events may drive ecology, rather than vice versa.
Speciation is an ongoing and commonplace process, occurring constantly and persistently around us.	It is only deemed to be rare by taxonomists, and the use of Latin binomials by ecologists is at best a crude approximation.
Environments are most appropriately defined by the ecology and genetics of the organisms themselves, and only indirectly by environmental measurements.	We can recognize three types of environments: external, ecological, and selective. Their measurement and interpretation have important consequences for population and evolutionary dynamics.
A population to an ecologist is not the same as it is to a geneticist.	Understanding the contrasting way in which the term is used is essential for unifying ecology and genetics.

netic variation has impacts on communities that go well beyond the species in which it is being measured. It is therefore likely that genetic variation is probably being quantified (and certainly conceptualized) inappropriately in conservation biology. It points out that conservation biologists must look beyond population genetics and perhaps more to community genetics in their thinking about diversity.

From an academic perspective, the featured papers illustrate that the insignia of community genetics proclaims that numerous questions remain unanswered with regard to the role of genetic variation in the functioning and composition of communities and ecosystems. Both papers point out that we need new levels of interpretation and new laws that scale to the level of the community rather than to the level of the single-species population. Neuhauser et al. (2003) contrast the classical "evolutionary ecology" approach of examining equilibrium/optimal situations with an approach that focuses on genetic and ecological dynamics in non-equilibrium situations. I found their paper particularly valuable in pointing out how explicitly manipulating the building blocks of community genetics can lead to outcomes different from those in which we assume that evolutionary ecology is a long and tempered dance. Whitham et al. (2003) take a more holistic approach, and show that genetic variation within keystone or dominant species can have cascading effects on the associated community and the ecosystem. They posit these effects as representing an "extended phenotype."

This interesting idea was presaged many years ago by the work of Maddox and Root (1990), who showed that clones of goldenrod plants could be characterized by their herbivores and by the genetic correlations among the herbivore abundances. However, I was still left unclear about whose phenotype was actually being extended. If genetic variation per se is the cause of new phenotypes at the community level, then is it the phenotype of the population that is being extended? How the heritability of a population property—as opposed to the heritability of, say, disease resistance—would be estimated needs to be fleshed out. Although there is no doubt that fitness effects of genes can interact via indirect community interactions, it may be premature to transfer genetic terms to a community context without the same rigor that has accompanied genetic thinking on gene interactions, linkage, and their consequences for genetic architecture.

It has obviously not been the intention of these papers to cover the field of community genetics comprehensively, and so it may be useful to point out some other issues and approaches that may gain momentum in the future. Coming from population and ecological genetics, two questions strike me as crucial. The first is whether, and to what degree, genetic recombination (as actualized in outcrossing and sexual reproduction) is responsible for maintaining population abundance. Much of the focus on discussions of the evolution of sex has been on the adaptive significance of sex, and on attempts to account for its maintenance, given its

“twofold” disadvantage. The converse question of how sex promotes species abundance is equally interesting, but, to my knowledge, has received almost no attention. *If we make one species genetically uniform, how abundant would it be (and how long would it persist) in a community?*

The second question addresses the extent to which genetic polymorphism is crucial for maintaining species diversity. Neuhauser et al. (2003) make a strong case that genetic polymorphism may be associated with species coexistence, and in support of this, they cite the experimental work of Lenski (2001) on phage/bacterial interactions (see also Bohannan and Lenski 2000). Whitham et al. (2003) show, with extensive examples from their own and other’s studies, that genetic variation within a dominant species can have community consequences. Translated to a more reductionist level, the question is whether species interactions involving genetic polymorphisms are more stable (vis a vis coexistence and mutual invasibility) than species interactions not involving such polymorphisms. This question is gaining tremendous applied significance as disease biologists struggle with how to interpret responses to drug and vaccine therapy in the face of within-pathogen strain variation. They term such collections of highly variable genotypes of a particular strain, or within a particular host, “quasi-species” (Eigen 1993), thereby acknowledging that when they speak of, say, a particular HIV infection within a host, this infection is not caused by a genetically uniform entity. Species more familiar to most ecologists also nearly always consist of races or ecotypes, and all have large amounts of genetic variation. It may be salutary for ecologists to preface (at least in their thoughts) any Latin binomial that they use by the qualifier “the quasi-species. . . .”! The term is already gaining acceptance in the context of computer simulations of coevolutionary processes (Savill and Hogeweg 1998). *If we generated a community consisting of randomly sampled asexual individuals that are genetically uniform within each species, would this community be as stable as one consisting of quasi-species?*

Coming more from a community ecology standpoint, I can again posit two questions that strike me as crucial. The first is the relationship between species diversity and genetic diversity. This is a question that I raised in my earlier description of community genetics (Antonovics 1992) and on which I presented some results from the studies of Morishima and Oka (1978) showing a positive relationship between genetic diversity and species diversity. There are few data exploring this relationship. The importance of genetics in biological invasions has also been emphasized for many years (Lee 2002), but one hardly hears discussion of these issues in the context of the larger community patterns of species diversity (i.e., latitudinal gradients). *Are species the right units for measuring community diversity, and how might we include, characterize, and measure*

the quasi-species component? How does diversity at this level influence community parameters?

In terms of global change, a major puzzle for me has always been why, given the huge potential for evolutionary change, the paleontological record has been useful in predicting climate change over tens of thousands of years or more. Surely, species have had the opportunity to evolve new tolerances and new distributions, and have been under pressure to do so. Their apparent conservatism remains a puzzle. Is it the result of sampling (i.e., only those species that show patterns concordant with other evidence are used in the analyses)? Is it because some species evolve less than others (if so why?)? Or is it because evolutionary changes are unable to keep pace with the rate of climatic change (Davis and Shaw 2002)? In the context of the paper by Whitham et al. (2003), we can also ask if community-level feedbacks through multispecies interactions impose constraints on evolution that are particularly severe for the dominant members of a community? Given the growing interest in food web evolution (Caldarelli et al. 1998), we can also ask if species occupying particular positions within food webs are more likely to evolve than others. *Can we identify species that have and have not responded genetically to past global change, and if so, what is their community context?*

Largely through the work of Hubbell (2001), ecologists are more accepting of the idea that speciation may be an important process in determining species diversity and species–area relationships. Presumably the Hawaiian *Drosophila* and the cichlid fishes of Africa were previously dismissed as special cases. If speciation does influence macroecological patterns, as indeed appears likely, then we must also ask to what extent mechanisms of speciation at the genetic level feed back into community structure. *Do some modes of speciation lead to more diverse communities than other modes?*

In conclusion, there are numerous exciting and challenging questions that can be brought under the flag of “community genetics.” The featured papers emphasize how thinking broadly about the genetical contexts in which species interact can lead to new insights and perspectives on community ecology. These insights have real and practical consequences for conservation, invasion biology, and disease control. I have also briefly tried to illustrate that there are many other fascinating questions in community genetics and no shortage of research directions for the future. Of course, the cynic in me notes that the insignia of “genetics” is itself rapidly fading, and that I should perhaps get an edge by positing the even newer discipline of “community genomics.” There are indeed many questions that we can ask about the genomic changes brought about by community interactions and the feedback between genomic change and ecology. What fractions of the genes in host organisms are involved in pathogen resistance? How old are these genes? What fractions

in pathogen genes are involved in immune evasion? Are genes determining host–pathogen interactions more duplicated and multiallelic than genes determining predator–prey interactions? What is the role that noncoding DNA plays in life history, phenology, and community interactions (the community DNA paradox!)? And so on. . . but then maybe one commentary is enough for now.

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