Ecology, 84(3), 2003, pp. 574–577

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-equilibrial 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

Manuscript received 8 July 2002; accepted 9 August 2002; Corresponding Editor: A. A. Agrawal. For reprints of this Special Feature, see footnote 1, p. 543.

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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 equilibrial 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 equilibrial 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.

ACKNOWLEDGMENTS

NSF Integrated Research Challenges in Environmental Biology grant IBN 9977063 supported preparation of the manuscript.

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Ecology, 84(3), 2003, pp. 577–580

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

Manuscript received and accepted 15 July 2002; final version received 15 August 2002. Corresponding Editor: A. A. Agrawal. For reprints of this Special Feature, see footnote 1, p. 543.

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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 (Dazsak and Cunningham 1999, Dazsak 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 competitive 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 distibution 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.

Acknowledgments

I thank Anurag Agrawal for giving me the opportunity to comment on the stimulating papers by Neuhauser et al. and Whitham et al. My musings were supported, in part, by NSF grant 9806427.

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Ecology, 84(3), 2003, pp. 580–582

SPECIAL FEATURE

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

Manuscript received 11 July 2002; accepted 14 July 2002; Corresponding Editor: A. A. Agrawal. For reprints of this Special Feature, see footnote 1, p. 543.

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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 insects), 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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Ecology, 84(3), 2003, pp. 583–585

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 × 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 1980*a*), and the surrounding ecological community (cf. examples in Whitham et al. 2003). With G × 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 × 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 populations 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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Manuscript received 26 June 2002; accepted 14 July 2002; Corresponding Editor: A. A. Agrawal. For reprints of this Special Feature, see footnote 1, p. 543.

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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 1980*b*) 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:

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

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 1980*a*, Wade and McCauley 1980, Goodnight 1991, Goodnight and Craig 1996, Wade and Griesemer 1998).

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Ecology, 84(3), 2003, pp. 586–588

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 homogenous 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 studies 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).

Manuscript received 1 July 2002; accepted 14 July 2002; final version received 15 August 2002. Corresponding Editor: A. A. Agrawal. For reprints of this Special Feature, see footnote 1, p. 543.

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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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Ecology, 84(3), 2003, pp. 588–591

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 reciprocality, 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 ‘‘keystone’’ 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 interactions 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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Manuscript received 25 June 2002; accepted 14 July 2002; final version received 15 August 2002. Corresponding Editor: A. A. Agrawal. For reprints of this Special Feature, see footnote 1, p. 543.

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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 (Avise 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!

ACKNOWLEDGMENTS

Jonathan Chase, Sylvia Fallon, Jonathan Losos, Bob Marquis, and Susanne Renner provided insightful discussion and made numerous helpful suggestions on the manuscript.

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Ecology, 84(3), 2003, pp. 592–597

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, McPeek 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 (McPeek 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 (McPeek 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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Manuscript received 19 July 2002; accepted 20 July 2002; final version received 15 August 2002. Corresponding Editor: A. A. Agrawal. For reprints of this Special Feature, see footnote 1, p. 543.

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ciation of pinyon pine (see Sultan 1995), depending on the spatial distribution and strength of different selection pressures (McPeek 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 cocolonize 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 (McPeek 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 × 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 km^2). 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 interspersion 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

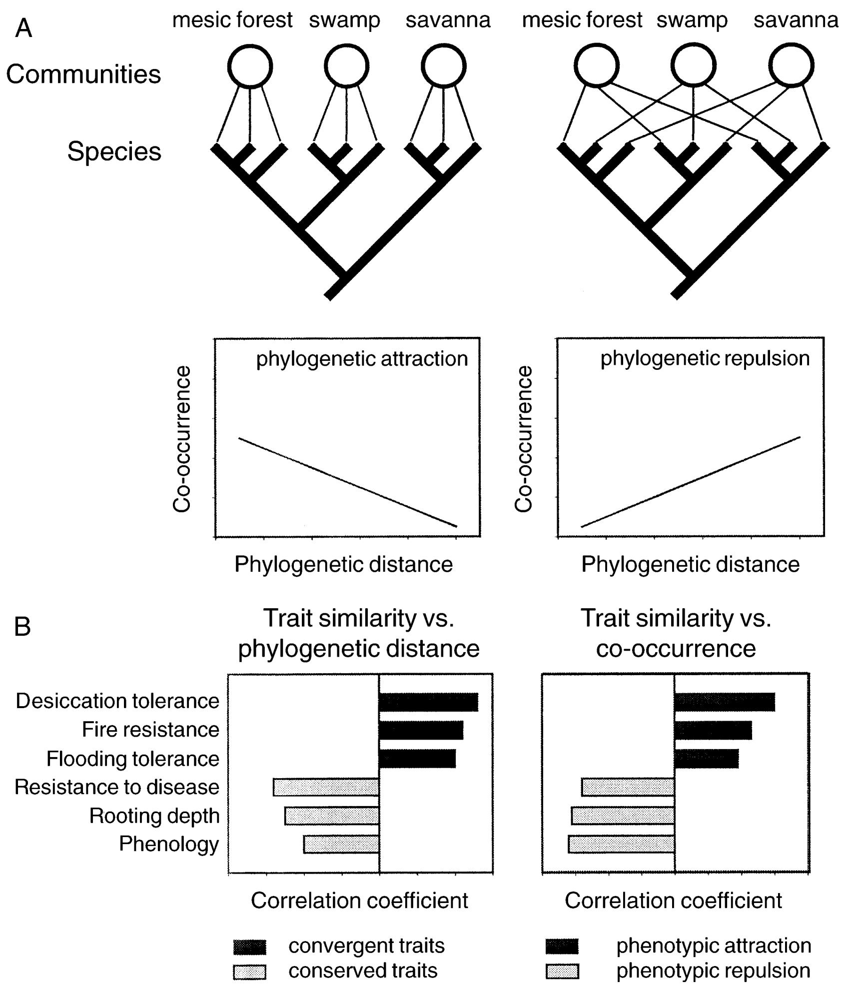

FIG. 1. (A) Alternative scenarios for the phylogenetic structure of communities. (B) Metrics to examine convergence and conservatism in trait evolution (left panel) and to identify traits that may be important in the assembly of communities (right panel).

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 environmental 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.

ACKNOWLEDGMENTS

The thoughts in this paper reflect numerous interactions with colleagues including David Ackerly, David Baum, Cam Webb, Michael Donoghue, and those involved in the NCEAS (National Center for Ecological Analysis and Synthesis) workshop on Phylogenetics and Community Ecology organized by Cam Webb and Michael Donoghue.

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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, Endler 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 Agriculature 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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Manuscript received and accepted 12 August 2002. Corresponding Editor: A. A. Agrawal. For reprints of this Special Feature, see footnote 1, p. 543.

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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 nonequilibrium 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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