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INTEGRATING MICRO- AND MACROEVOLUTIONARY PROCESSES IN COMMUNITY ECOLOGY

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Introduction

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

The incorporation of phylogenetic analysis in community ecology (e.g., Brooks and McLennan 1991, Ricklefs and Schluter 1993, Losos 1996, 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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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

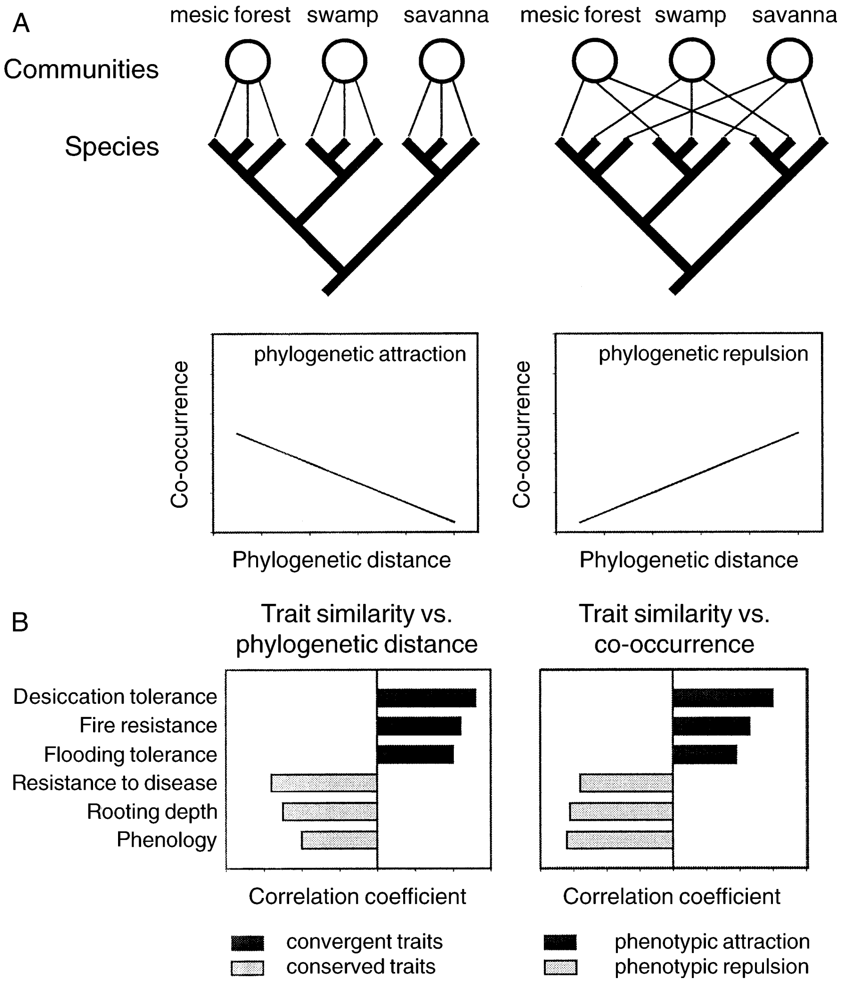

FIG. 1. (A) Alternative scenarios for the phylogenetic structure of communities. (B) Metrics to examine convergence and conservatism in trait evolution (left panel) and to identify traits that may be important in the assembly of communities (right panel).

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.

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Literature Cited

Ackerly, D. D. 1999. Phylogeny and the comparative method in plant functional ecology. Pages 391–413 *in* M. Press, J. D. Scholes, and M. G. Barker, editors. Physiological plant ecology. Blackwell Scientific, Oxford, UK.

Ackerly, D. D., and M. J. Donoghue. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). American Naturalist **152**:767–791.

Agrawal, A. 2001. Phenotypic plasticity in the interactions and evolution of species. Science **294**:321–326.

Bazzaz, F. A. 1996. Plants in changing environments: linking physiological, population, and community ecology. Cambridge University Press, Cambridge, UK.

Böhning-Gaese, K., and R. Oberrath. 1999. Phylogenetic effects on morphological, life-history, behavioural and ecological traits of birds. Evolutionary Ecology Research **1**: 347–364.

Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, ecology and behavior. University of Chicago Press, Chicago, Illinois, USA.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–310 *in* P. J. den Boer and G. R. Gradwell, editors. Dynamics of numbers in populations. Center for Agricultural Publishing and Documentation, PUDOC, Wagenigen, The Netherlands.

Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution **18**:586–608.

Etterson, J., and R. Shaw. 2001. Constraint to adaptive evolution in response to global warming. Science **294**:151–154.

Farrell, B. D. 1998. ''Inordinate Fondness'' explained: why are there so many beetles? Science **281**:555–559.

Jablonski, D., and J. J. Sepkoski. 1996. Paleobiology, community ecology, and scales of ecological pattern. Ecology **77**:1367–1378.

Janz, N., K. Nyblom, and S. Nylin. 2001. Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. Evolution **55**:783–796.

Janz, N., and S. Nylin. 1998. Butterflies and plants: a phylogenetic study. Evolution **52**:486–502.

Janzen, D. 1970. Herbivores and the numbers of tree species in tropical forests. American Naturalist **104**:501–528.

Kelley, S. T., and B. D. Farrell. 1998. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bard beetles (Scolytidae). Evolution **52**:1731–1743.

Labandeira, C. C., and J. J. Sepkoski. 1993. Insect diversity in the fossil record. Science **261**:310–315.

Lawrence, M. J. 2000. Population genetics of homomorphic self-incompatibility polymorphisms in flowering plants. Annals of Botany **85**:221–226.

Losos, J. B. 1996. Phylogenetic perspectives on community ecology. Ecology **77**:1344–1354.

Losos, J., T. Jackman, A. Larson, K. DeQueiroz, and L. Rogriguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science **279**:2115–2118.

Manos, P. S., and M. J. Donoghue. 2001. Progress in northern hemisphere phytogeography: an introduction. International Journal of Plant Sciences **162**:S1–S2.

McPeek, M. A. 1996. Linking local species interactions to rates of speciation in communities. Ecology **77**:1355–1366.

McPeek, M. A., and T. E. Miller. 1996. Evolutionary biology and community ecology. Ecology **77**:1319–1320.

Neuhauser, C., D. A. Andow, G. E. Heimpl, G. May, R. G. Shaw, and S. Wagenius. 2003. Community genetics: expanding the synthesis of ecology and genetics. Ecology **84**: 545–558.

Parrish, J. A. D., and F. A. Bazzaz. 1976. Niche separation in roots of successional plants. Ecology **57**:1281–1288.

Ricklefs, R. E., and D. Schluter. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.

Schlichting, C. D. *In press.* The role of phenotypic plasticity in diversification. *In* T. J. DeWitt and S. M. Scheiner, editors. Phenotypic plasticity: functional and conceptual approaches. Oxford University Press, Oxford, UK.

Schluter, D. 2000. Ecological character displacement in adaptive radiation. American Naturalist **156**:S4–S16.

Silvertown, J., M. Dodd, and D. Gowing. 2001. Phylogeny and the niche structure of meadow plant communities. Journal of Ecology **89**:428–435.

Sultan, S. E. 1995. Phenotypic plasticity and plant adaptation. Acta Botanica Neerlandica **44**:363–383.

Sultan, S. E., and H. G. Spencer. 2002. Metapopulation structure favors plasticity over local adaptation. American Naturalist **160**:271–283.

Wade, M. J. 2001. Infectious speciation. Nature **409**:675–677.

Wagner, G. P., and L. Altenberg. 1996. Complex adaptations and the evolution of evolvability. Evolution **50**:967–976.

Webb, C. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist **156**:145–155.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics **33**:475–505.

Weiher, E., G. Clarke, and P. Keddy. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. Oikos **81**:309–322.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics **20**:249–278.

Whitham, T. G., W. P. Young, G. D. Mortinsen, C. A. Gehring, J. A. Schweitzer, S. M. Shuster, G. M. Wimp, D. G. Fischer, J. K. Bailey, R. L. Lindroth, S. Woolbright, and C. R. Kuske. 2003. Community genetics: a consequence of the extended phenotype. Ecology **84**:559–573.

Wills, C., R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. Proceedings of the National Academy of Sciences (USA) **94**:1252–1257.

Zangerl, A. R., and M. R. Berenbaum. 1993. Plant chemistry, insect adaptations to plant chemistry, and host plant utilization patterns. Ecology **74**:47–54.