

EVOLVING METACOMMUNITIES: TOWARD AN EVOLUTIONARY PERSPECTIVE ON METACOMMUNITIES

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Abstract. The metacommunity framework predicts that local coexistence depends on the outcome of local species interactions and regional migration. In analogous fashion, spatial structure among populations can shape species interactions through evolutionary mechanisms. Yet, most metacommunity theories assume that populations do not evolve. Here, we evaluate how evolution shapes local species coexistence and exclusion within the multiscale and multispecies context embodied by the metacommunity framework. In general, coexistence in joint ecological–evolutionary models requires low to intermediate dispersal rates that can promote maintenance of both regional species and genetic diversity. These conditions support a set of key mechanisms that modify patterns of species coexistence including local adaptation, gene storage effects, genetic rescue effects, spatial genetic subsidies, and metacommunity evolution. Multispecies extensions indicate that correlated selection can further alter the outcome of interspecific interactions depending on the magnitude and direction of correlations and shape of fitness trade-offs. We suggest that an evolving metacommunity perspective has the potential to generate novel predictions about community structure and function by incorporating the genetic and species diversity that characterize natural communities. In adopting such a perspective, we seek to facilitate understanding about the interactions between evolutionary and metacommunity dynamics.

Key words: *adaptation; coexistence; community interactions; contemporary evolution; evolutionary ecology; gene flow; metacommunity; microgeographic dispersal; multispecies perspective; trade-offs.*

INTRODUCTION

Predictions of species coexistence typically focus on either local (Hutchinson 1959, Tilman 1985) or regional processes (Levins 1969, Hanski 1999). Nevertheless, joint consideration of both local dynamics and regional movement can improve upon single-scale predictions (Mouquet and Loreau 2002). Recent theories integrate multiscale processes by defining their operational unit, the metacommunity, as a set of local communities linked by the dispersal of multiple potentially interacting species (Wilson 1992, Leibold et al. 2004). Besides incorporating a spatial dimension, metacommunity theories also consider the multispecies interactions found in natural communities. By integrating multiscale and multispecies investigations in community ecology, the metacommunity

framework is generating novel insights and stimulating innovative experiments (Leibold et al. 2004, Holyoak et al. 2005). Metacommunity theory generally has been successful in refining our understanding of how spatially integrated mechanisms can alter local community dynamics and patterns of local species diversity. These mechanisms include interspecific trade-offs between local interactions and dispersal (patch dynamics perspective; Levins and Culver [1971], Yu and Wilson [2001]), matching of species to fitness-maximizing environments via migration (species sorting; Chase and Leibold [2003]), ecological rescue effects dependent on regionally similar, but locally heterogeneous, fitness (mass effects; Amarasekare and Nisbet [2001], Mouquet and Loreau [2002]) and interspecific fitness equivalence (neutral; Hubbell [2001]). Although these spatial processes do not universally stabilize species coexistence (see Holt 1993), they provide a set of mechanisms useful for predicting outcomes of local interactions distributed among multiple sites.

Interspecific trait variation offers a commonly cited mechanism that modifies species coexistence in meta-

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community models (but see Hubbell 2001). Just as traits can vary among species, the traits of populations and individuals also show substantial variation (Thompson 1998). This intraspecific genetic variation is often maintained through local selection and migration among heterogeneous patches (Levene 1953, Bulmer 1972, Lenormand 2002, Kawecki and Ebert 2004). From an evolutionary perspective, models of adaptive trait variation without spatial structure or population dynamics may ignore potentially important drivers of trait dynamics (Antonovics et al. 1997, Lively 1999, Gandon 2002). Therefore, incorporating the regional metacommunity perspective into existing evolutionary models has the ability to improve predictions of trait variation across space.

At the same time, we think that evolution will make important contributions to the developing metacommunity framework. Evolution has the potential to alter the operation of mechanisms assumed to underlie metacommunity dynamics. Adaptation and maladaptation can change how populations partition heterogeneous resources in space, thereby transforming a potential mechanism of coexistence in species-sorting and mass-effects metacommunities. Moreover, evolution of dispersal or habitat preference can modify community connectivity, the regional feature that often determines metacommunity dynamics (Holyoak et al. 2005). As compared to abiotic selection, biotic selection can differ in its effects on coexistence, given the likelihood for complex coevolutionary trait dynamics (Thompson 1994, Lively 1999, Gandon 2002). Dispersal and reciprocal demographic changes in interacting species can elicit novel dynamics attributable to biotic selection (Gomulkiewicz et al. 2000, Kawecki and Holt 2002, Holt et al. 2004). Indirect interactions among multiple species can alter evolutionary trajectories from those involving pairwise interactions (Nuismer and Doebeli 2004, Strauss and Irwin 2004). Incorporating evolution into metacommunity theory provides a logical next step for the framework's development. Consequently, ecologists increasingly recognize the need to include evolution in metacommunity theories (Antonovics et al. 1997, Hanski and Heino 2003, Wade 2003, Whitham et al. 2003, Amarasekare et al. 2004, Holt 2005, Leibold et al. 2005, Thompson 2005).

Previous reviews have greatly improved our understanding of spatially varying traits involved in pairwise interactions (Thompson 1994, 1999, Whitham et al. 2003, Hanski and Gaggiotti 2004). Here, our primary objective is to facilitate linkages between multispecies metacommunity demographics and evolution. We use the term "evolving metacommunity" to refer to a set of local communities linked by the dispersal of multiple potentially interacting species in which genetically determined trait variation within species modifies the outcome of interspecific interactions. We assume that evolving metacommunities can reach ecological and evolutionary equilibrium, but that perturbations fre-

quently reinitiate transient dynamics. In contrast to the geographic mosaic theory of coevolution (Thompson 2005), we shift the focus from using spatial patterns of selection and gene flow to explain gene frequencies to a focus on using evolutionary mechanisms to explain emergent ecological properties such as local and regional species richness and abundance, trophic structure, productivity, and ecosystem function. This shift is supported by an expanding body of theoretical and empirical research that shows how evolution modifies the properties of both communities and ecosystems (Kondoh 2003, Benkman and Siepielski 2004, Loeuille and Loreau 2004, Schweitzer et al. 2004, Hairston et al. 2005, Vellend 2005, 2006).

For this review, we address the specific objective of predicting local patterns of species diversity in an evolving metacommunity framework. We describe five evolutionary-ecological mechanisms that enhance or diminish the potential for coexistence among species. We then extend our review to include emerging research on multispecies metacommunities. In the last section, we delineate opportunities for future theoretical development and empirical assessment. We assume a patch-dynamics perspective that applies to many mosaic habitats including ponds, lakes, isolated vegetation stands, islands, and forest fragments (Thompson 1999, Leibold and Norberg 2004, Urban 2004). We consider evolution attributed to interspecific interactions as modified by local environmental conditions. In our usage, evolution encompasses the more specific coevolutionary effects due to reciprocal selection. We assume that interspecific interactions can evolve directly, in response to other species traits (e.g., prey morphological defenses and predator morphology), or indirectly, in response to patch-specific context (e.g., prey crypsis). We include the various outcomes of natural selection that can arise at multiple spatial scales ranging from local communities to regional metacommunities. Local species diversity can be shaped both by the interface between local adaptation and migration and by regional adaptations to the spatial distance between, and distribution of, habitat types. Prey populations that evolve defenses against specific predator species exemplify adaptations to local community interactions (Reznick et al. 1990, Cousyn et al. 2001, McPeck et al. 2001). Regional adaptations such as dispersal rate or habitat preference can directly influence metacommunity structure by altering connectivity among patches for genetically diverged populations (Hanski et al. 2004). Lastly, we recognize that maladaptation frequently can shape the outcome of species interactions (Thompson et al. 2002). We expect that maladaptation will be a pervasive component of evolutionary dynamics in metacommunities due to the framework's emphasis on migration as a driver of community structure. As an example, the interplay between locally adapted resistance and virulence and gene-flow-induced maladaptation figures prominently in predicting regional

coexistence of host–pathogen interactions (Gandon et al. 1996, Antonovics et al. 1997, Lively 1999, Burdon and Thrall 2000).

AN EVOLUTIONARY COMMUNITY ECOLOGY?

Although community ecology historically has been dominated by a species-centric viewpoint, ecologists increasingly find value in population-level perspectives (Antonovics 1992, Luck et al. 2003, Whitham et al. 2003). This approach is supported by evidence for biotic selection mosaics, adaptive trait variation among local populations, and linked community and evolutionary dynamics. Spatially variable biotic selection can generate complex selection mosaics for metacommunity assembly (Thompson and Cunningham 2002, Urban 2004). Populations often exhibit microgeographic adaptations (Skelly 2004) such that traits differ among heterogeneous patches separated by less distance than average individuals disperse (Storfer and Sih 1998, Zangerl and Berenbaum 2003). Genetic variation within species affects community structure (Booth and Grime 2003, Hughes and Stachowicz 2004, Wimp et al. 2004) and provides the capacity for species interactions to evolve within the time scale of ecological dynamics (Pimentel 1968, Thompson 1998, Cousyn et al. 2001, Yoshida et al. 2003, Hairston et al. 2005). Hence, community dynamics often may require evolutionary explanations.

Furthermore, metacommunity theories generally assume that more than two species coexist in communities. Multispecies interactions can alter ecological and evolutionary dynamics from those assuming pairwise interactions through indirect or nonadditive effects (Stinchcombe and Rausher 2002, Strauss and Irwin 2004). Many interacting species provide opportunities for diffuse evolution where complex genetic correlations mold trait dynamics, interacting species modify the operation of biotic selection, or community context alters genetic variance–covariance matrices (Stinchcombe and Rausher 2002, Strauss et al. 2005). Empirical research provides evidence for correlated selection among interaction traits (reviewed in Strauss and Irwin [2004]) and differential gene expression in dissimilar community contexts (Stinchcombe and Rausher 2002). Interaction traits may regularly depend on community diversity.

Lastly, we explore the analogous operation of ecological and evolutionary mechanisms on diversity patterns. In general, the processes assumed to shape metacommunity assembly in niche-oriented models, species sorting among heterogeneous patches and migration, have evolutionary analogues in natural selection and gene flow (Amarasekare 2000, Norberg 2004, Holt 2005, Leibold et al. 2005, Vellend and Geber 2005). A population's demography and genetic composition both depend on the rates at which processes create and reduce local variation among units, a process that may improve the match between traits and environments (via species sorting and natural selection)

(Pimentel 1968, Levins 1969, Levin and Udovic 1977, Amarasekare 2000, Holt 2005, Leibold et al. 2005, Vellend and Geber 2005). Migration and gene flow also can operate in a similar manner. Just as intermediate migration rates promote species coexistence in mass-effects metacommunity models of competitors (Mouquet and Loreau 2002), intermediate gene flow can maintain local genetic diversity (Gandon et al. 1996, Thrall and Burdon 1999, Vellend 2005). By facilitating asynchronous dynamics of unstable local interactions, intermediate connectivity (via migration and gene flow) supplies a mechanism of potential coexistence shared by models of structured population genetics, metapopulations, metacommunities, and metacommunity genetics (Hanski 1999, Thrall and Burdon 1999, Amarasekare 2000, Gomulkiewicz et al. 2000, Gandon 2002, Mouquet and Loreau 2002, Leibold et al. 2005, Vellend and Geber 2005). The similar operation of ecological and evolutionary processes on diversity is consistent with spatial coexistence models that assume identical forms whether populated by genotypes or species (May and Nowak 1994, Amarasekare 2000). Analogous ecological and evolutionary processes could prove redundant in their effects on community dynamics if they were to operate in the same way and at commensurate spatial and temporal scales. However, the more likely scenario is one in which differences in the outcome of, and relative spatial and temporal scaling of, ecological and evolutionary processes generate complex feedback loops that alter predictions produced by each mechanism alone (Lively 1999, Gomulkiewicz et al. 2000, Gandon 2002, Leibold et al. 2005). Hence, interactions between genetic and species diversity and the processes that shape them frequently may generate departures from existing metacommunity theory.

SPATIAL PERSPECTIVES ON EVOLUTION IN COMMUNITIES

Models of species interactions can be differentiated by their assumptions about patch heterogeneity. Two categorical effects can arise by considering spatial contributions to evolutionary and ecological community dynamics. First, coupling homogeneous environments by movement can increase effective population sizes, prolong transient dynamics, and permit asynchronous regional dynamics to stabilize local interactions (Holt and Gomulkiewicz 1997, Gandon 2002, Hanski and Gaggiotti 2004, Holt et al. 2004, Holyoak et al. 2005). Second, interpatch heterogeneity can alter dynamics by introducing variation in the fitnesses of species or genotypes (Hochberg and van Baalen 1998, Vellend 2005). Both effects, those due to space *per se* and those due to environmental variation, can drive evolutionary dynamics (Thrall et al. 1998, Hanski and Gaggiotti 2004, Holt et al. 2004, Holt 2005).

Evolutionary community models also differ in their inclusion of population demography. Much theory has focused on trait dynamics while disregarding associated demographic effects. However, exceptional work ad-

dresses joint evolutionary and demographic dynamics in spatially connected communities (Gandon et al. 1996, Antonovics et al. 1997, Hochberg and van Baalen 1998, Thrall and Burdon 1999, Nuismer and Kirkpatrick 2003). Research that incorporates both demography and evolution in metacommunities originates from community genetics, metapopulation genetics, and the geographic mosaic theory of coevolution. We next briefly review these theories.

Levins' (1969) pioneering metapopulation model evaluated the consequences of genetically heterogeneous predator-prey populations for their persistence in a set of homogeneous patches. However, it was not until the early 1990s that the metacommunity emerged as distinct from the metapopulation (Wilson 1992). At this time, evolution was becoming increasingly enmeshed with nascent metacommunity theory. Early models by Frank (1991, 1993) found that recurrent migration could stabilize the joint ecological and evolutionary dynamics of host-parasite interactions by reintroducing advantageous genes. Theory incorporating multiple homogeneous patches pointed toward the importance of dispersal for determining trait and host-parasite population dynamics in "interaction metapopulations" (reviewed in Thrall and Burdon [1997]). Further research elucidated the role of variable migration rates or distances among interacting species in driving adaptation and the potential for local coexistence (Gandon et al. 1996, Thrall and Burdon 1997, Gandon 2002). Recent extensions of metapopulation genetics to multiple species illustrate how adaptations to regional distributions of host patches impact consumer persistence (Kuussaari et al. 2000, Hanski and Heino 2003).

The geographic mosaic theory of coevolution (GMTC) was developed to predict how spatially heterogeneous selection molds the evolution of species interactions (Thompson 1994). The GMTC incorporates three hypotheses: (1) interspecific selection mosaics produce variable evolutionary trajectories; (2) divergent evolutionary trajectories lead to the presence (hotspots) or absence (coldspots) of coevolution; and (3) trait mixing, colonization-extinction dynamics, and drift generate maladaptation (Thompson 1999). The GMTC incorporates environmental heterogeneity in addition to space per se in determining the outcome of species interactions in disparate patches (Nuismer and Kirkpatrick 2003). Empirical investigations support GMTC tenets, verifying the generality of selection mosaics (Benkman et al. 2001, Brodie et al. 2002, Zangerl and Berenbaum 2003), coevolutionary hotspots and coldspots (Benkman et al. 2001, Brodie et al. 2002), and the effect of gene flow on co-adaptation (Forde et al. 2004). Of particular note, the GMTC predicts that evolutionary mechanisms can govern species coexistence (Thompson 1999, Siepielski and Benkman 2004).

This work has been accompanied by a growing appreciation for the importance of genetics in shaping communities (Antonovics 1992). Research on commu-

nity genetics demonstrates how variation within dominant or keystone species can structure dependent community and ecosystem processes (Whitham et al. 2003). Laboratory experiments have separated the disparate influences of intra- and intercommunity selection on evolutionary outcomes and species coexistence, thus providing support for hierarchical selection in structured communities (Goodnight and Craig 1996, Wade and Goodnight 1998, Wade 2003). This concept has since been expanded to suggest that community and ecosystem consequences of genetic variation form an organism's "extended phenotype" (Wade 2003, Whitham et al. 2003).

Metapopulation genetics, the GMTC, and community genetics continue to enhance our understanding of evolution within metacommunities. As metacommunity theory has become more advanced, hypotheses generated by these frameworks can now be applied to understand and to predict interactions between evolutionary and metacommunity dynamics. An evolving metacommunity perspective provides an explicit theoretical framework from which to predict species diversity and community and ecosystem function as informed by the biological realities of spatial connectance and multispecies communities. Research on evolutionary ecological processes can thereby inform metacommunity theory by grounding ecological explanations in evolutionary mechanisms.

EVOLUTIONARY-ECOLOGICAL MECHANISMS OF COEXISTENCE AND EXCLUSION

Interactions between ecological and evolutionary mechanisms in space may enhance or diminish the potential for local coexistence through various integrated mechanisms. We review five interrelated mechanisms that have emerged from theoretical research: local adaptation, the gene storage effect, genetic rescue effect, spatial genetic subsidies, and metacommunity adaptation (Fig. 1). This list is preliminary. Ongoing research undoubtedly will uncover additional ways in which joint ecological and evolutionary mechanisms can shape species diversity.

Local adaptation

Local adaptation can either promote or diminish species coexistence in evolutionary models by altering the outcome of local interactions (Abrams 2000, Case and Taper 2000, Holt 2003, Nuismer and Doebeli 2004). The magnitude and direction of interspecific interactions and migration rates determine whether biotic adaptation will promote or undermine community coexistence (Holt 2003, Nuismer and Doebeli 2004). Pimentel (1968) suggested that the adaptation of a victim population could regulate the size of an expanding enemy population and ensuing local species diversity via a genetic feedback. Interacting pathogens and hosts generally became locally adapted and more likely to persist when they migrated more than their counterparts in coevolutionary models (Gandon et al. 1996, Gandon 2002,

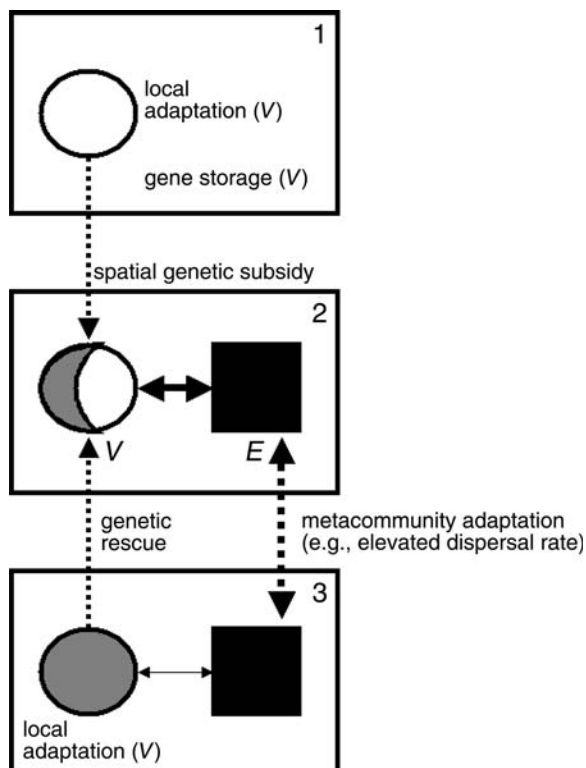


FIG. 1. Selected evolutionary mechanisms of coexistence in a victim-enemy interaction. Where the enemy population (E) interacts with the victim population (V) in patches 2 and 3, the enemy affects victim survival in proportion to the size of interaction (solid) arrows. Dashed arrows indicate migration. A fitness trade-off occurs depending on whether individuals express a defensive trait (gray phenotype) in the presence or absence of the enemy. In patch 1, the victim population has undergone local adaptation to conditions absent the enemy (white phenotype). Enemy-free patch 1 provides for the gene storage effect for the victim's nonpredator phenotype. Immigration of maladapted victims from patch 1 to 2 provides a spatial genetic subsidy to the enemy population. Immigration of victims adapted to the enemy (gray phenotype) from patch 3 to 2 could produce the genetic rescue effect if gene flow prevents extirpation of victims in patch 2. Throughout the set of linked communities, the enemy population has developed increased dispersal abilities to take advantage of maladapted victim populations (metacommunity adaptation).

Thrall and Burdon 2002). Coexistence in this context depends on the continuous and reciprocal modification of interactions through repeated cycles of adaptation and maladaptation (Lively 1999). Nuismer and Kirkpatrick (2003) also showed that intermediate host gene flow could promote adaptation and subsequent coexistence along an abiotic gradient of fitness optima for hosts and parasites.

In other cases, local adaptation may diminish local species diversity. A single species can dominate a metacommunity if it evolves a globally fit trait that counters the potential for coexistence via interspecific trade-offs (May and Nowak 1994). Adaptation in a

population can lead to its own extirpation when coupled with demographic cycles among interacting species (Matsuda and Abrams 1994, Pels et al. 2002). An important determinant of so-called evolutionary suicide is frequency-dependent selection that operates until a genetic or demographic limit is reached and further fitness gains are impossible (Roughgarden 1976, Matsuda and Abrams 1994). In species range models, adaptation to a source habitat can reduce a species' overall niche breadth through a positive feedback called "migrational meltdown," in which asymmetries in population size enhance relative gene flow into sinks (Ronce and Kirkpatrick 2001). This gene flow, in turn, further increases maladaptation and population asymmetry. In general, local adaptation to source habitats can limit local adaptation in sinks and restrict the use of alternate niches (reviewed in Holt [2003]). In community models, parasite extinction is possible because local adaptations cannot efficiently track host genotypes without sufficient migration and/or mutation (Gandon et al. 1996, Thrall and Burdon 1999, Nuismer and Kirkpatrick 2003). Diverse exploitation strategies can evolve in predators, and this leads to the overexploitation of prey and eventual collapse of both populations (Pels et al. 2002). Adaptation of new species along an abiotic gradient compresses existing species ranges and reduces overlapping zones of coexistence (Case and Taper 2000).

Gene storage effect

The gene storage effect relies on the capacity for regional spatial structure to harbor local genetic diversity from the homogenizing effects of local selection (Wright 1969). This regional genetic diversity, in turn, enables the continual reintroduction of genes that previously had been lost from patches. The "storage" of currently maladaptive genes by metacommunity structure (akin to the ecological storage effect; Chesson [1994]) allows them to be reintroduced into a population when they might be favored again by fluctuating selection imposed by interacting populations (Fig. 1) (Hamilton 1993, Judson 1995, Gandon et al. 1996). Gene storage effects can alter local species diversity by rescuing populations from local extirpation (genetic rescue effect) and by safeguarding the genetic variation necessary to respond to dynamic selection (Hamilton 1993, Gandon et al. 1996, Lively 1999).

Genetic rescue effect

Although ecological models often invoke a rescue effect to explain local persistence via immigration, the genetic rescue effect promotes population persistence via immigration of adapted individuals into a maladapted population (Antonovics et al. 1997). In several host-parasite examples, local dynamics between genetically variant enemies and victims were stabilized by low-to-intermediate migration rates or more localized spatial scales of dispersal (Gandon et al. 1996, Antonovics et al. 1997, Thrall et al. 1998). In these models, immigration of

more fit genotypes rescued maladapted populations from the extinction threat imposed by intense fluctuating selection. Selection mosaic models suggest an analogous situation, whereby habitats with limited interspecific interactions (coldspots) facilitate regional species coexistence despite intense and unstable interactions in hotspots (Gomulkiewicz et al. 2000). However, a practical difficulty arises in separating out the demographic effects of genetic rescue from those attributed to maladapted interacting populations given coupled coevolutionary dynamics (Thompson et al. 2002). In most cases, rescue effects will arise both from the immigration of adapted genotypes and from ensuing maladaptation of resident interacting populations.

Spatial genetic subsidies

Regional maintenance of genetic variation also can generate spatial genetic subsidies whereby the flow of maladapted victims into a habitat increases the resources available to a local enemy population (Fig. 1) (Holt 2005, Leibold et al. 2005). Maladapted prey immigrants can promote local coexistence by providing a subsidy of easily exploited resources for predators living among locally adapted prey (Hochberg and van Baalen 1998). In a comparable scenario, a spatial refuge for susceptible hosts enhanced disease persistence in a simulated host metapopulation by providing maladapted victims for infection by disease populations (Antonovics et al. 1997). Spatial genetic subsidies imply that maladapted populations living in marginal or sink habitats can prove integral for maintaining regional coexistence (Hochberg and van Baalen 1998). However, despite inputs of maladapted victim resources, enemy persistence is not assured because resources may not be sufficient to support predators (Hochberg and van Baalen 1998), or high resource inputs can lead to rapid exploitation followed by population crashes (Pels et al. 2002, Thrall and Burdon 2002). Nonetheless, spatial genetic subsidies provide a potentially important stabilizing mechanism for species coexistence in victim–enemy communities linked by high dispersal rates (Holt et al. 2005, Leibold et al. 2005).

Metacommunity adaptation

Broader scale adaptations to regional interpatch distances and community distributions also can influence patterns of species coexistence. Traits influencing colonization rate may often evolve and, in turn, alter predictions of metapopulation persistence (Hanski 1999, Gyllenberg and Metz 2001, Heino and Hanski 2001, Rousset and Ronce 2004) or a species' niche breadth and range (Ronce and Kirkpatrick 2001, Holt 2003). Dispersal ability can evolve depending on costs/benefits associated with emigration in landscapes that differ in their interpatch distances (Hanski et al. 2004). Habitat preference also can alter colonization rates in specific patches, thereby modifying the outcome of local interactions (Hanski and Heino 2003). In one predator–prey model, predators persisted by evolving inter-

mediate migration rates and consumption rates (Pels et al. 2002). Heterogeneous environments also can promote the evolution of phenotypic plasticity (Sultan and Spencer 2002). Phenotypic plasticity can facilitate species coexistence by providing a flexible solution to existing or novel community variation (Pigliucci and Murren 2003, Price et al. 2003).

A MULTISPECIES PERSPECTIVE

Understanding the ecological implications of multispecies evolution is an exciting frontier for future theoretical development (Nuismer and Doebeli 2004). Currently, most models explore either pairwise interactions or multispecies evolution without spatial context. Nonspatial models generally suggest that correlated selection among three or more species generates novel trait dynamics. In a nonspatial multispecies model, Nuismer and Doebeli (2004) found that correlated multispecific selection created divergent evolutionary equilibria and dynamics, depending on selection strength and interaction type. This multispecific selection generated trade-offs between adaptations to multiple species, such that the focal interacting species underwent recurrent maladaptation (Nuismer and Doebeli 2004). Adding a co-pollinator to a pairwise host–pollinator interaction simultaneously altered selection magnitude and sign and drove coevolutionary trajectories in associated interaction traits (Gomulkiewicz et al. 2003). In food web models, evolution can generate positive complexity–stability relationships and enhanced flexibility to environmental fluctuations (Kondoh 2003), and can alter the importance of top-down vs. bottom-up control (Loeuille and Loreau 2004). Models without spatial structure suggest that multispecies evolution modifies predictions from pairwise interaction models. However, the extent of modification depends on specific assumptions, such as the magnitude and shape of trade-offs and form of selection.

Although many models explore ecological–evolutionary dynamics in two-species metacommunities, few explicitly evaluate multispecies selection in space. Exceptions include metapopulation models of multispecies competition and multiple infections (May and Nowak 1994) that predict how colonization, competition, and mutation affect pathogen diversity. Although not originally constructed to evaluate joint species and population dynamics, the assumed process of mutation–competition sorting could apply to asexual clonal species sharing similar ecological niches. Given a strict hierarchy of competitive dominance, these models predict increasing regional coexistence as long as different types can continue to subdivide phenotypic space into finer compartments (May and Nowak 1994). A quantitative-genetics species range model suggests a similar pattern whereby ecologically similar species distribute themselves into increasingly smaller ranges along a productivity gradient (Case and Taper 2000). Additional species compress constituent range sizes while maintain-

ing coexistence in zones of overlap. In a multispecies competitive metacommunity assuming heterogeneous patches and varying species and phenotypic optima, Vellend (2005) found that species coexistence and the strength of correlation between genetic and species diversity were shaped by habitat area, migration rate, and environmental heterogeneity. An important result from this simulation was that the relative regional species abundances determined the influence of habitat characteristics. Hence, regional abundance offers a promising means to classify the importance of evolutionary dynamics for different metacommunity species. In another evolving metacommunity model that assumed coevolutionary interactions among competing species, increasing genotypic diversity and niche range within species enhanced local species diversity (Vellend 2006). However, increasing the range of genotypes that competed strongly with one another diminished local species diversity. Multispecies competition models generally predict that adding new genetic variants, as defined by their differential use of patchy resources, can facilitate maintenance of species within interconnected and heterogeneous patches. Relaxing the prevailing assumptions of simple asexual genetic architecture found in most of these models could elicit novel outcomes (Vellend 2005). For instance, Case and Taper's (2000) model illustrates how quantitative genetic models can be used to address such questions.

A multispecies perspective adds substantial complexity to theoretical models. Progress toward understanding evolution in metacommunities will be constrained by trade-offs between analytic tractability and biological complexity. Therefore, both pairwise interaction models and multispecies models with simplifying assumptions will be necessary to develop understanding from an evolving metacommunity perspective.

EMPIRICAL RESEARCH

Results from two research programs indicate the valuable insights that emerge through empirical work on evolving multispecies interactions. Benkman's (2001) study on lodgepole pines demonstrates the interdependency of coevolution and community composition. Without pine squirrels, selection on pines by crossbills has led to the development of longer and narrower cones with thick scales that enhance their defense against bird predation. In concert, reciprocal selection on crossbills has initiated evolution of large, decurved bills that elevate their feeding rates on pinecones. Where squirrels outcompete crossbills, squirrel predation selects for pines with wider cones and fewer seeds. Pine cone borer moths further modify interactions by selecting for smaller cones with fewer seeds (Siepielski and Benkman 2004). These coevolutionary changes promote competitive interactions between moths and squirrels for the same cone morphology and, as a result, can decrease moth abundances in stands with squirrels (Siepielski and Benkman 2004). Similarly, Newfoundland crossbills

became threatened by extinction once introduced red squirrels outcompeted them for spruce cones not adapted to squirrel predation (Parchman and Benkman 2002). Thus, interspecific competition affects coevolutionary dynamics, whereas multispecies coevolution governs the coexistence of seed predators.

Research from community genetics suggests that genetically diverse dominant species can shape coexistence in dependent communities, a situation that may apply to many macroparasites and host-specific herbivores (Mopper et al. 2000, Whitham et al. 2003). These guilds depend on host phenotypes, which can vary dramatically over microgeographic scales (Dungey et al. 2000, Mopper et al. 2000). For instance, a narrow (100-m) hybrid genetic mixing zone between two *Eucalyptus* species that differ in chemical defenses generated a central peak in insect and fungal community diversity (Dungey et al. 2000). An individual cottonwood's genetic diversity determined its arthropod community composition (Wimp et al. 2004), whereas stand genetic variation predicted local arthropod diversity (Wimp et al. 2004). Moreover, evidence suggests that the cottonwood's genetic landscape may lead to subsequent herbivore adaptations (McIntyre and Whitham 2003). In general, genetic mosaics of host individuals can generate sets of evolving dependent communities, maladaptation following host colonization, and genetically determined colonization-extinction dynamics (Mopper et al. 2000, McIntyre and Whitham 2003).

An exciting and rapidly emerging field with extensions to metacommunity theory explores how evolution shapes ecosystem processes. Squirrels in pine forests select for reduced pinecone serotiny, a trait that facilitates seedling recruitment after fires (Benkman and Siepielski 2004). Hence, squirrel selection on pines could alter community succession and ecosystem processes following fire. In a similar manner, genetic variation among cottonwoods influences leaf tannin concentrations (Schweitzer et al. 2004). Tannin variation, in turn, affects leaf litter decomposition and net soil nitrogen mineralization rates (Schweitzer et al. 2004). Hence, evolving community interactions not only influence the demographics of interacting species, but also can alter underlying ecosystem function.

OUTLOOK

The coexistence of species and genes depends on the interplay of analogous ecological and evolutionary processes that generate new variation, either by immigration or local evolution, and that reduce variation through local extirpation, natural selection, or drift (Leibold and Norberg 2004, Leibold et al. 2005). Today, evidence supports a set of observations, hypotheses, and predictions underlying an evolving metacommunity perspective: (1) diverse communities and heterogeneous landscapes generate a complex selection mosaic for metacommunity assembly (Urban 2004, Leibold et al. 2005, Thompson 2005); (2) these selection mosaics can

produce adaptation and maladaptation, depending on gene flow (Amarasekare 2000, Gandon 2002, Thompson et al. 2002, Kawecki and Ebert 2004); and (3) joint evolutionary and demographic dynamics can shape local species coexistence and exclusion (Thompson 1999, Nuismer et al. 2003, Hairston et al. 2005, Vellend 2005). Feedbacks are possible between genetic and species diversity, given contemporary and microgeographic evolution of species interactions. To understand the importance of these feedbacks, we must first discern the conditions under which evolution is necessary to predict species coexistence and when evolution can be ignored. Testing this evolving metacommunity perspective poses significant challenges. Yet we suggest that the mechanistic insights gained will improve ecological predictions.

A starting point is to evaluate the ecological consequences of adding genetic variation to existing metacommunity models. In this way, we can begin to determine if evolution alters classic metacommunity predictions. These efforts may generate novel predictions, especially when allowing for multispecies interactions and explicit space. Nevertheless, complexities intrinsic to an evolving metacommunity perspective impose practical limitations on finding analytic solutions. In some cases, advancements in analytic tools may allow solutions previously confined to simulations (Gandon 2002). However, analyses often will rely on parameterized simulations. Rapidly increasing computational efficiency facilitates the exploration of sizeable parameter spaces. However, dependence on simulations reemphasizes the need to determine sensitive parameters, especially the shapes of trade-off functions, to encourage cross-validation between theoretical and empirical research (Abrams 2001, Loeuille and Loreau 2004).

An evolving metacommunity perspective offers a number of hypotheses for theoretical and empirical exploration. Just as migration provides an organizing principle for understanding divergent metacommunity dynamics (Leibold et al. 2004), gene flow often may structure the outcome of evolution in metacommunities by determining patterns of adaptation and maladaptation. Simple predictions of coexistence or exclusion at multiple spatial scales may be possible by scaling spatial variation in selection relative to species' dispersal distances. For example, understanding finer scale variation in co-adaptation and maladaptation in cross-bills, squirrels, and pines (Siepielski and Benkman 2004) could provide valuable insights into broader geographic patterns by deepening our understanding of the scaling of evolutionary and ecological processes. Second, evolution's influence on trophic and ecosystem properties remains unexplored. In many cases, emergent ecological properties may be shaped by evolutionary mechanisms (Loeuille and Loreau 2004, Hairston et al. 2005). Lastly, the evolving metacommunity perspective directs empiricists to record genetic frequencies and species abundances over the timescales at which species reproduce and the spatial scales over which individuals

disperse. Such long-term studies of trait and demographic variation can provide tools for discriminating the relative importance of temporal and spatial processes in determining community dynamics (Lively 1999, Lively and Jokela 2002). An evolutionary perspective also requires novel experiments that alter connectivity between model metacommunities (Brockhurst et al. 2003, Forde et al. 2004) or that manipulate genetic variation among interacting species in constructed communities (Booth and Grime 2003, Hughes and Stachowicz 2004). We suggest that such empirical measurements will reveal that genetic, phenotypic, and environmental variation mutually determine ecological patterns across heterogeneous landscapes.

The divide between ecological and evolutionary thought stems from long-standing debates about whether satisfactory ecological theory can be developed without recourse to evolution (Orians 1962, Thompson 1998). These distinctions can artificially isolate evolutionary and ecological mechanisms that often operate together in nature (Hairston et al. 2005, Holt 2005, Thompson 2005). On one hand, metacommunity theory provides a conceptual framework for predicting community properties from a spatially integrated perspective. Recent advancements in metacommunity theory offer a set of mechanisms that predict outcomes of interspecific interactions by considering the interplay between regional trade-offs in fitness, asynchronous regional dynamics, and patch heterogeneity. To date, these mechanisms have lacked grounding in basic evolutionary principles. On the other hand, few evolutionary models of species interactions have addressed how trait evolution shapes community diversity and function from the regional perspective embodied in metacommunity theories. A unified approach, made possible by advancements in genetic techniques and computational technologies, suggests a promising role for an evolving metacommunity perspective. By considering evolution among multiple species and explicitly examining spatial connections among communities, the evolving metacommunity perspective has the potential to generate novel predictions about the mechanisms of community diversity, assembly, function, and dynamics across complex landscape mosaics. Testing this framework will require integrated research programs that seek to explain community structure using data ranging from landscape heterogeneity to the genetic architecture of ecologically relevant traits. Such endeavors undoubtedly will entail extensive collaborations and long-term commitments from granting agencies (Antonovics 1992, Thompson 1999). We believe that these efforts, given the chance, will be amply rewarded. We suspect that an integrated biology will uncover many cases in which ecology and evolution cannot be considered in isolation. To an extent not generally appreciated, the evolutionary theater (Hutchinson 1965) often may be indistinguishable from the ecological play.

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