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Maladaptation and Mass Effects in a Metacommunity: Consequences for Species Coexistence

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ABSTRACT: Metacommunity theories predict multispecies coexistence based on the interplay between local species interactions and regional migration. To date, most metacommunity models implicitly assume that evolution can be ignored. Yet empirical studies indicate a substantial potential for contemporary evolution. I evaluate how evolution alters species diversity in a simulated mass-effects (sink-source) metacommunity. Populations inhabiting source habitats became locally adapted, while subordinate competitors became maladapted because of assumed ecological and phenotypic trade-offs between habitats. This maladaptation decreased and leveled relative abundances among subordinate populations. These two effects produced two regions of departure from nonevolutionary predictions. Assuming low proportional migration, maladaptation reduced local species richness via an overall reduction in reproductive rates in sink populations. With intermediate proportional migration, a greater absolute reduction of reproductive rates in intermediate competitors leveled reproductive rates and thereby enhanced local species richness. Although maladaptation is usually viewed as a constraint on species coexistence, simulations suggest that its effects on diversity are manifold and dependent on interpatch migration and community context. Hence, metacommunity predictions often may profit from an evolutionary perspective. Results indicate that modifications of community connectivity, such as might occur during habitat fragmentation, could elicit rapid shifts in communities from regions of high to low biodiversity.

Keywords: metacommunity, local adaptation, maladaptation, sink-source, patch dynamics, evolutionary ecology.

The remarkable diversity of natural communities motivates fundamental questions about the mechanisms that

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sustain multispecies coexistence. For species that share resources, competitive interactions can exclude all but the most superior competitors in the absence of stabilizing mechanisms. Multispecies competitive coexistence is possible, however, if competing species differentially partition shared resources (Hutchinson 1959; Chase and Leibold 2003) or if species have similar fitnesses (Hubbell 2001). A synthetic approach allows for the differential partitioning of resources among heterogeneous local environments while maintaining equivalent species fitnesses at the regional metacommunity scale (Mouquet and Loreau 2002). In this metacommunity view, migration among heterogeneous patches integrates the mechanisms responsible for local competitive dynamics and the regional redistribution of species and individuals (Leibold et al. 2004; Holyoak et al. 2005). The metacommunity framework offers a promising tool for understanding the biological complexities of multispecies interactions and spatial heterogeneity found in real communities. Ongoing development of metacommunity ideas is generating novel predictions about community structure in relation to regional species pools, community trait variation, environmental gradients, and migration (reviewed by Leibold et al. [2004]; Holyoak et al. [2005]).

Despite their promise, most metacommunity models implicitly assume that evolution does not influence ecological dynamics. This assumption is at odds with a growing body of empirical evidence suggesting that evolution can occur within timescales relevant to community dynamics (Thompson 1998), that genetic and species diversities are interdependent (Vellend and Geber 2005), and that evolution can alter the outcome of interspecific interactions (Yoshida et al. 2003; Siepielski and Benkman 2004). Analogous movement of species and genes between patches is expected to initiate concurrent shifts in species and genetic compositions (Levins 1969; Antonovics 1992; Gandon et al. 1996; Hochberg and van Baalen 1998; Gomulkiewicz et al. 2000; Thompson et al. 2002; Vellend 2005). Evolutionary and ecological mechanisms often interact and thereby alter predictions of coexistence generated by each mechanism alone (Hochberg and van Baalen 1998; Lively 1999; Gomulkiewicz et al. 2000; Gandon 2002;

Nuismer and Kirkpatrick 2003; Vellend and Geber 2005). Hence, evolutionary mechanisms also may alter predictions made by metacommunity models that omit the possibility of evolved responses (Mouquet and Loreau 2003; Amarasekare et al. 2004; Urban and Skelly 2006).

Model simulations explored here bridge the gap between mass-effects metacommunity models of species diversity (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002, 2003) and single-species models of sink-source evolution (Kawecki and Stearns 1993; Kawecki et al. 1997; Ronce and Kirkpatrick 2001; Holt 2003). "Mass effects" refers to an extension of sink-source dynamics that is applied to multispecies metacommunities when migration from high- to low-fitness communities alters the recipient community's dynamics (Shmida and Wilson 1985; Mouquet et al. 2005). Metacommunity models including mass effects demonstrate that migration can promote local species richness by redistributing species that differ in local competitive abilities but converge in their regional fitness (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002). However, the ecological outcomes of mass effects depend critically on assumed levels of migration. Simulations predict that local species richness will be greatest with intermediate proportional migration (fig. 1*a*; Mouquet and Loreau 2002). Mass-effects models have generated empirical tests (Mouquet et al. 2004), motivated theoretical extensions (Loreau et al. 2003), and contributed to the development of an important metacommunity perspective (Leibold et al. 2004). However, these models have yet to address the implications of genetic diversity for species coexistence.

From an evolutionary standpoint, population asymmetry induced by sink-source structure can render selection inefficient in sink habitats, which, in turn, can lead to maladaptation (Kawecki and Stearns 1993; Holt and Gomulkiewicz 1997; Kawecki et al. 1997; Kirkpatrick and Barton 1997; Ronce and Kirkpatrick 2001; Kawecki and Holt 2002). Results from continuous-range (Kirkpatrick and Barton 1997; Case and Taper 2000; Holt 2003) and discrete-patch dynamics (Ronce and Kirkpatrick 2001) models indicate that maladaptation induced by asymmetrical gene flow can generate limits to species' ranges and can promote niche conservatism. One way this can occur is through "migrational meltdown," whereby equal proportional gene flow from source to sink populations leads to a greater absolute transfer of maladapted genotypes into sinks, which, in turn, decreases sink population size and further increases population asymmetry (Ronce and Kirkpatrick 2001). Under special circumstances, the possibility remains for range expansion, assuming adequate genetic variation and a shallow selection gradient (Kirkpatrick and Barton 1997). But asymmetrical gene flow into sink habitats more generally leads to maladaptation (Lenormand

2002; Thompson et al. 2002; Holt 2003; Kawecki and Ebert 2004). In such cases, regional phenotypes evolve to reflect the relative demographic contributions of divergent patches to the regional metapopulation (Houston and McNamara 1992; Kawecki and Stearns 1993).

In principle, adaptation can promote the coexistence of competing species and enhance local biodiversity by improving the match between species and local conditions (Pimentel 1968; May and Nowak 1994; Tilman 1994). In a recent multispecies lattice model, increasing genetic diversity minimized competitive exclusion by promoting a more efficient matching of species to available niche space (Vellend 2006). However, as both gene flow and population asymmetry increase, such selection can be expected to become increasingly inefficient in sink habitats (Holt 1996, 2003; Kirkpatrick and Barton 1997; Ronce and Kirkpatrick 2001). Even moderate gene flow can lead to migrational meltdown and create a spiraling decline in sink population size and fitness (Ronce and Kirkpatrick 2001). The demographic consequences of maladaptation could promote coexistence by freeing habitat for inferior competitors. However, maladaptation also could lower population abundances to levels that elevate extinction risks. A review of perturbation theory in sink-source systems predicts that low migration rates can promote both genetic and species richness, assuming that competitive rankings trade off across heterogeneous patches (Amarasekare 2000). However, high migration rates are expected to prevent species and genetic coexistence by synchronizing dynamics across patches and eliminating system heterogeneity (Amarasekare 2000). Although instructive, separate predictions for genes and species may not inform outcomes when genetic variation affects species diversity (Vellend and Geber 2005). At the same time, evolutionary-ecological models of single-species (e.g., species range models; Holt 2003) or pairwise interactions (e.g., Gandon et al. 1996; Gomulkiewicz et al. 2000; Gandon 2002; Nuismer et al. 2003) may not reliably predict emergent properties of multispecies communities because of complex indirect interactions (Gomulkiewicz et al. 2003; Nuismer and Doebeli 2004; Urban and Skelly 2006). Therefore, the question remains: does maladaptation promote or diminish local species richness in a mass-effects metacommunity?

To address this question, I modified an existing mass-effects model (Mouquet and Loreau 2002, 2003) to include adaptive phenotypic variation in the reproductive rates of 20 competing species inhabiting 20 heterogeneous patches. Simulations suggest that maladaptation can both enhance and diminish local species richness in a metacommunity, depending on proportional migration. Different migration-dependent effects arose because of two demographic effects of maladaptation that simultaneously diminished and lev-
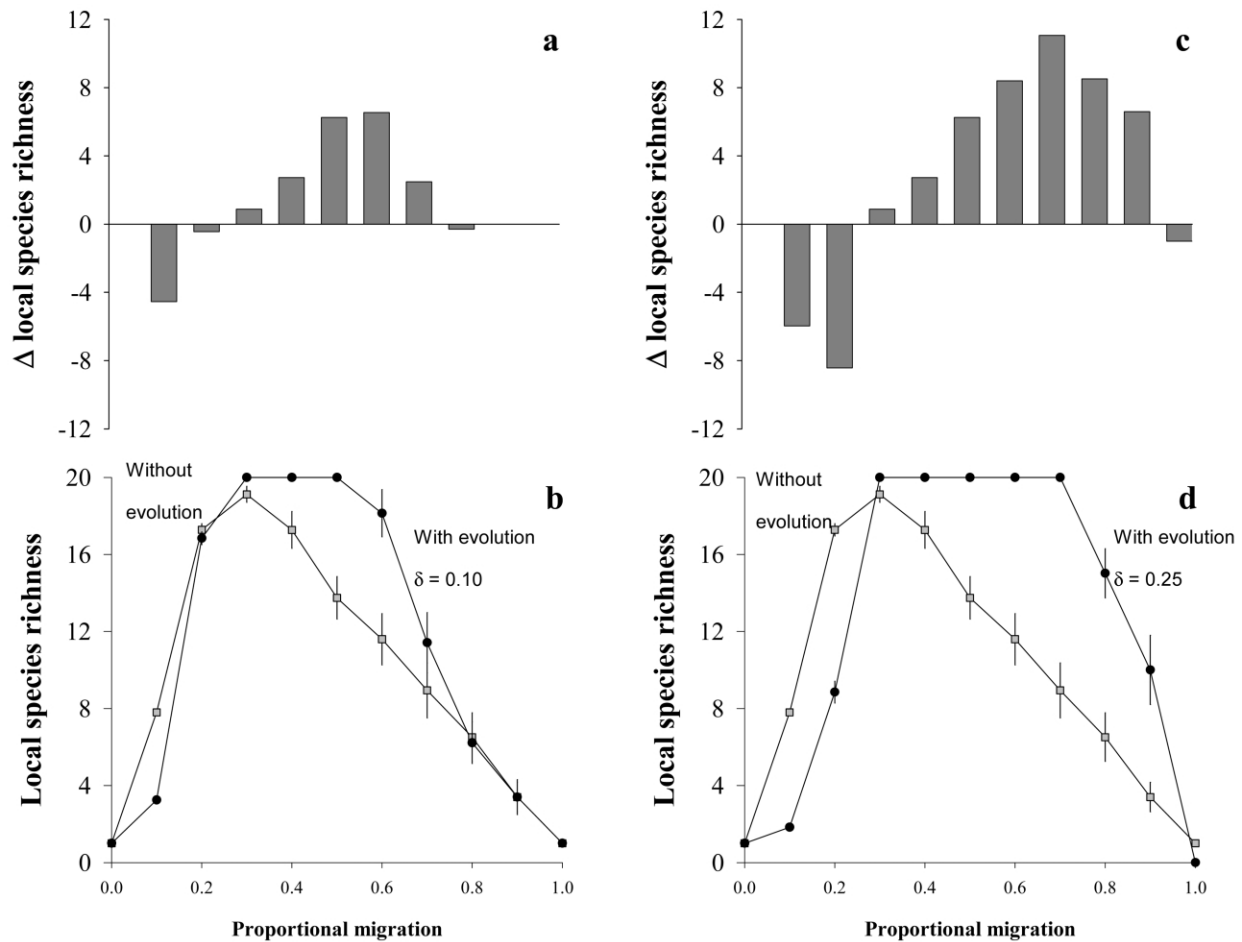
Figure 1: *a, c,* Change in local species richness between the two models (evolutionary minus original model) as a function of proportional migration, assuming a fitness increment (δ) of 10% (*a*) or 25% (*c*) relative to patch-specific potential reproductive rates. *b, d,* Local species richness (± 1 SD) with (*circles*) and without (*squares*) evolution. The evolutionary model assumes a phenotypic trade-off between natal and emigrant phenotypic fitnesses.

eled population abundances among subordinate competitors. Model outcomes were based on a relatively simple characterization of genetics and thus may have general implications for predicting species diversity in evolving metacommunities.

Methods

I retained all parameters and assumptions of an earlier mass-effects metacommunity model (Mouquet and Loreau 2002, 2003) to facilitate comparisons between evolutionary and existing nonevolutionary models. Details of simulation procedures can be found in the appendix in the online edition of the *American Naturalist*. Briefly, this mass-effects metacommunity model assumes that individuals compete for space in a lottery model that is enmeshed within a spatially implicit finite-island model of migration. Each species experiences variable potential fitness among patches because of heterogeneous environmental contexts (i.e., resources, predation, and abiotic factors) but similar fitness averaged across the region. In the absence of migration, the mass-effects metacommunity model predicts that the fittest species in each patch will exclude all others. However, adding migration to the model allows locally poor competitors to coexist in local patches via emigration from source habitats. In the model, 20 species compete for space in 20 (N) communities. The proportion of microsites P occupied by each species i within patch k depends on a community-wide symmetric immigration rate a, patch- and species-specific reproductive rates c_{ik}, the

proportion of locally available microsites V_k in each patch (1 minus the sum of all P_i), and a constant and instantaneous mortality rate m:

$$\frac{dP_{ik}}{dt} = \left[\frac{a}{N-1}\left(\sum_{l \neq k}^{N} c_{il}P_{il}\right) + (1-a)c_{ik}P_{ik}\right]V_k - mP_{ik} \quad (1)$$

(Mouquet and Loreau 2002, 2003).

Patch- and species-specific potential reproductive rates followed a competitive hierarchy such that each species was characterized by a similar regional fitness when reproductive rates were averaged over all communities (regional fitness equivalence assumption). This competitive hierarchy of species within a habitat could be envisioned to result from interspecific trait variation in species' abilities to exploit spatially varying resources or defend themselves against different patch-specific communities of predators, parasites, or pathogens. Consistent with the mass-effects metacommunity model, I added a stochastic element to competitive rankings by randomly adding or subtracting 5% from all potential reproductive rates to provide a more realistic and stochastic competitive hierarchy (Mouquet and Loreau 2002). A species was considered extinct when its proportional representation in a community fell below 0.01 (Mouquet and Loreau 2002).

For the evolutionary model, I assumed that individuals were characterized by variable proportions of phenotypes that described their reproductive rates under varying patch-specific environmental conditions. Individuals that evolved the highest reproductive rate for a given species and in a particular environment were considered locally adapted. Those individuals with phenotypes less fit than the optimum were considered locally maladapted. Note that by local maladaptation, I specifically refer to the divergence of fitness from local rather than global optima. I incorporated these assumptions by modifying equation (1) to track the proportion of individuals occupying microsites in each of five phenotypic classes (z):

$$\frac{dP_{ikz}}{dt} = \left[\frac{a}{N-1}\left(\sum_{l \neq k}^{N} c_{ilz}P_{ilz}\right) + (1-a)c_{ikz}P_{ikz}\right]V_k$$
$$+ f(\mu) - mP_{ikz}, \quad (2)$$

where $f(\mu)$ refers to a mutation submodel. In the mutation submodel, I assumed that each phenotype was determined by the sum of four biallelic additive loci coded 1 or 0 (e.g., Heino and Hanski 2001) and modeled the resultant neutral evolution based on a transition probability matrix weighted by each phenotype's relative abundance in the population (see appendix for details). The model of phenotypic evolution assumed to operate in the simulation

was consistent with simple additive quantitative genetic structure and haploid asexual reproduction. I assumed that each individual expressed one of five phenotypes ($z = 0$–4), which were passed to the next generation depending on their relative abundance in the surviving population of each species. The reproductive rate of each individual was determined by its ranked phenotype relative to its potential ecological optimum in a given habitat. For all species, the phenotype $z = 4$ was set to the site-specific fitness optimum corresponding to the values used in the original mass-effects metacommunity model. For each subsequent phenotype of lower rank, an equal and proportional fitness reduction δc_{ik} was assigned. To evaluate the relative influence of these fitness reductions, I varied δ from 5% to 25%, which produced a maximum potential maladaptation range across the five phenotypes of 20%–100%. This potential maladaptation spans the range found empirically when divergent phenotypes are expressed in antagonistic communities (13%–95%; M. C. Urban and D. K. Skelly, unpublished data). Maladaptation, as described here, refers to a population's distance from its maximum potential fitness peak (Crespi 2000; Thompson et al. 2002). Together, adaptation and maladaptation describe a population's relative fitness: one population may be better adapted to local conditions than another (closer to its adaptive peak) but still be considered maladapted to a degree determined by its deviance from the optimum.

Adding phenotypic variation to the mass-effects metacommunity model required that I specify the relationship between a phenotype's fitness in its natal patch and its fitness in a newly colonized, heterogeneous patch. I modeled this relationship as a within-species trade-off between varying trait optima among heterogeneous patches, given the operation of antagonistic selection (Lenormand 2002). Note that this phenotypic trade-off is in addition to the ecological trade-off assumed in the original model. Each change in environmentally determined potential fitness reduced the fitness of emigrant phenotypes by one fitness reduction (δ) along the existing environmental gradient. For example, an individual that emigrated to a patch with a maximum species reproductive rate one rank lower than its natal habitat had its phenotypic reproductive rate reduced by one fitness decrement. Migration into each patch of higher-rank change (and thus assumed to constitute increasingly divergent selection environments) received fitness decrements of two, three, four, and five, after which all emigrants were assigned to the lowest fitness class. These changes in fitness along an environmental gradient would apply to natural situations where a species' phenotype determines its (evolutionary) fitness in a manner congruous to an interspecific (ecological) fitness gradient. This type of phenotypic trade-off is consistent with negative genetic correlations among multiple traits suited for different envi-
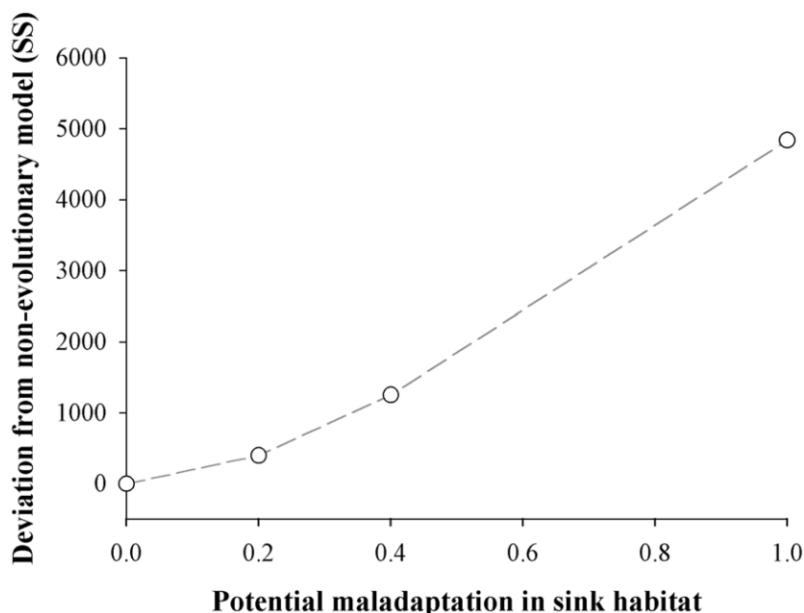
Figure 2: Deviation from the nonevolutionary mass-effects metacommunity model in local species richness for the interaction between model type (original vs. evolutionary model) and migration rate (0–1.0), as measured by sums of squared deviations. Results are shown for a range of different values of maximum potential maladaptation. All deviations were significantly different from the original model ($p \ll .0001$).

ronments. For model simplicity, I assumed that migration occurred after selection such that populations became adapted to local conditions before migrating into a new environment. Therefore, I ignored the effect of immediate migration to a foreign patch and back into the original patch without loss of fitness. Based on low probabilities of such an exchange, deviations from this assumption would have little effect on model outcomes. I also evaluated bracketed model alternatives, including one where I assumed no trade-off and one where I assumed zero fitness in all emigrants (see appendix for details).

Results

Local and Regional Coexistence

Antagonistic selection and gene flow produced substantial maladaptation in populations inhabiting a mass-effects (sink-source) metacommunity. This maladaptation generated significant departures from the original model without evolutionary dynamics under all levels of assumed potential genetic variation (evolutionary vs. mass-effects metacommunity model: $F = 59.6–1,544.6$, df $= 1, 528$, $p < .00001$; model × migration: $F = 56.5–779.6$, df $= 10, 528$, $p < .00001$). Maladaptation initiated by gene flow reduced local species richness at low proportional migration levels ($a = 0.1–0.2$) and enhanced local species richness at intermediate to high proportional migration levels

($a = 0.3–0.9$; fig. 1). Local species richness dropped from 7.8 ± 0.1 in the mass-effects metacommunity model ($\delta = 0$) to 1.8 ± 0.1 in the evolutionary model ($\delta = 0.25$) at a proportional migration of 10%. In addition, all 20 species could coexist in a patch for a substantial portion of the migration parameter space (0.3–0.7) in the evolutionary model, while at least some species were always excluded in the original model. The predictions made by the evolutionary model became increasingly divergent from those of the original model as potential maladaptation increased from 0% to 100% (fig. 2). Regional (gamma) species richness was higher in the evolutionary model than in the mass-effects metacommunity model, assuming intermediate to high migration (fig. 3; $a = 0.5–0.9$). Maladaptation generally increased the migration parameter space over which the entire regional species pool was retained. Beta diversity in the evolutionary model was also higher at low migration ($a = 0.1–0.2$) and lower at intermediate migration levels ($a = 0.3–0.7$).

Species Abundance Patterns

In the evolutionary model, the highest-ranked competitor in each source habitat became locally adapted by maintaining a reproductive rate close to its optimal value (fig. 4). Maladaptation reduced the reproductive rates of all subordinate (rank 2 or lower) species in each patch. The
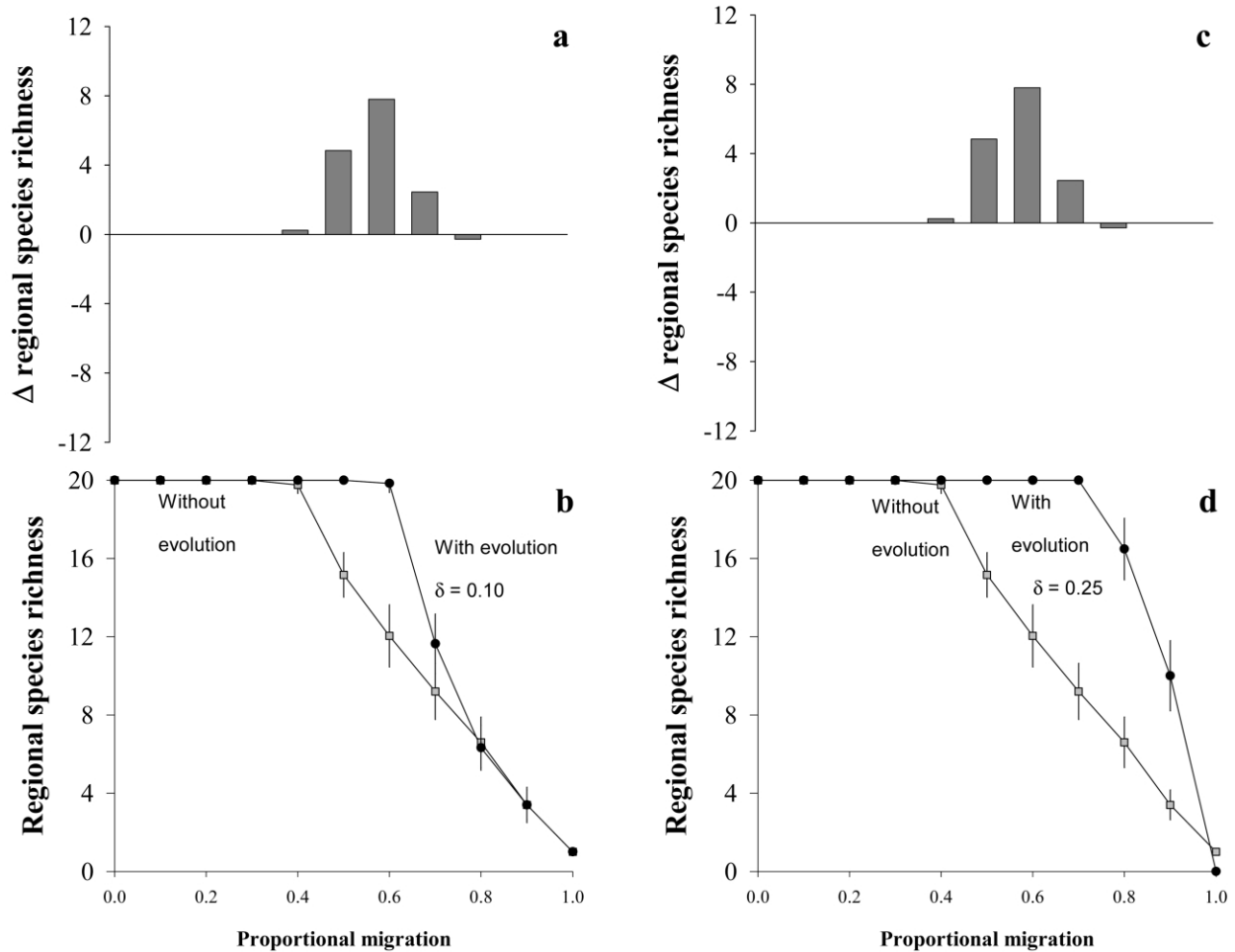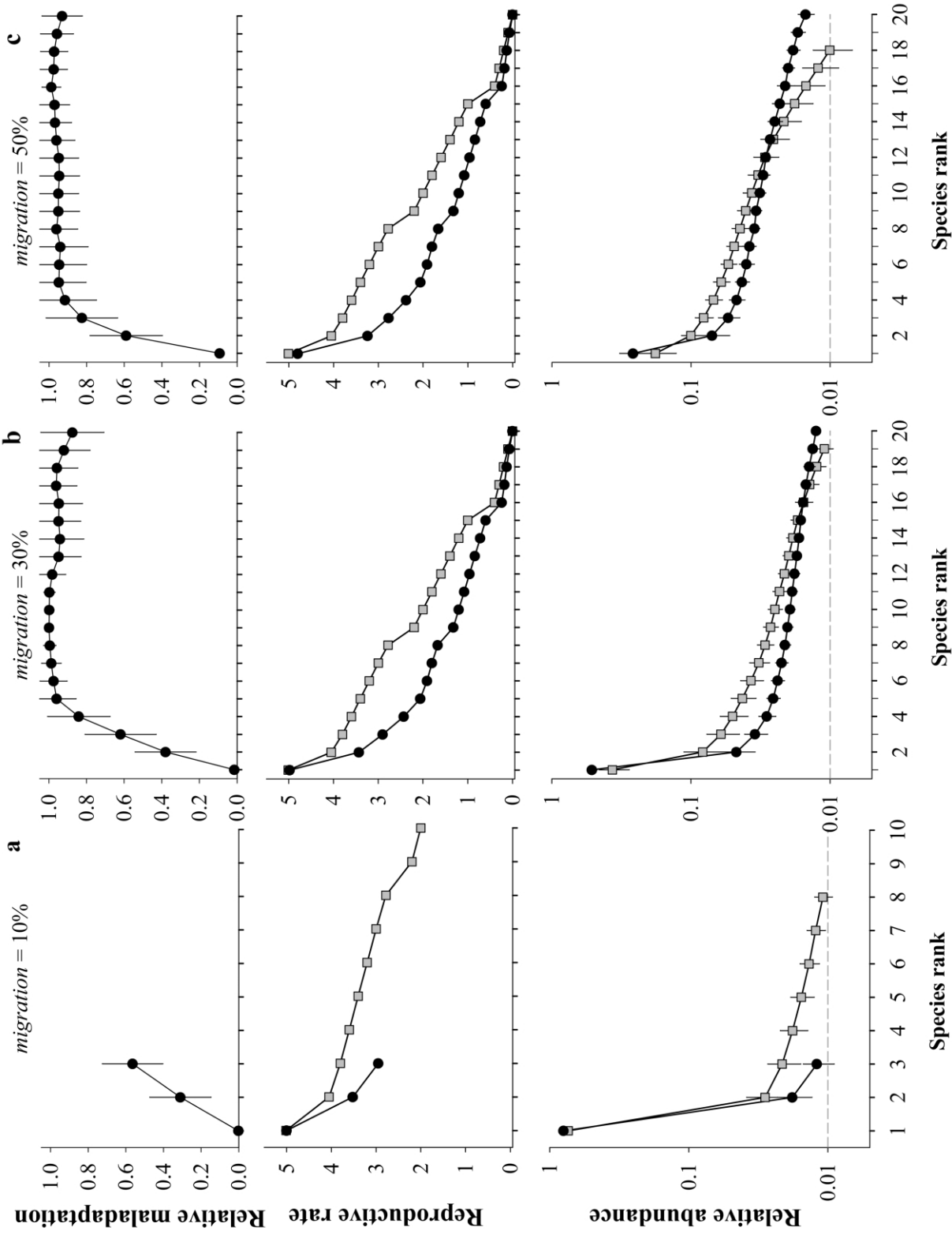
Figure 3: Change in (evolutionary minus original) model (*a, c*) and realized (*b, d*) regional (metacommunity) species richness (±1 SD) with (*circles*) and without (*squares*) evolution in relation to proportional migration. Parameters and fitness decrements among phenotypes are as in figure 1.

demographic effects of maladaptation in the model can be understood in two stages. First, maladaptation through high gene flow decreased the reproductive rates of subordinate competitors by a proportional amount. This decline in subordinate species translated into lower overall abundances in subordinate and higher abundances in source (adapted) populations after translation of reproductive rates into population abundances under the zero-sum assumption. Second, the absolute reduction in reproductive rates differed depending on the relative competitive ranking of species. Higher-ranked but still subordinate species suffered a greater absolute decline in reproductive rate than low-ranked species because of the proportional fitness trade-off assumption (fig. 4*b*, 4*c*). Therefore, maladaptation had a leveling effect on the abundances of subordinate (sink) populations in each patch. This leveling effect, combined with the zero-

assumption, meant that more species could coexist with than without maladaptation. These two demographic effects varied in their influence on community diversity depending on assumed levels of proportional migration. Assuming low proportional migration, the overall decline in rank abundances due to maladaptation accounted for more populations falling below the extinction threshold (fig. 4*a*). With intermediate migration, the leveling effect of maladaptation on intermediate competitors decreased the extinction probabilities of poor competitors and opened space for their persistence in sink habitats (fig. 4*b*, 4*c*). This outcome depended on their maintenance by migration from source habitats in the metacommunity.

Model Assumptions

Results depended on the proportional fitness trade-off assumption. Assuming no phenotypic trade-offs between al-

ternative patches produced patterns consistent with the original model. Assuming a stronger phenotypic-trade-off model in which each phenotype was specialized on a particular patch and had zero fitness in all others resulted in patterns similar to those generated by the more moderate phenotypic-trade-off gradient assumed here (appendix). This suggests that results are robust to a lower number of phenotypic states, because the strong-trade-off model results in phenotypes that are either maximally adapted or maladapted. Patterns remained unchanged in simulations where I set the potential phenotypic distribution to the mean $\pm$ 50% of values found in the original model. Thus, model outcomes also were robust to the distribution of phenotypes. Finally, mutation had a relatively minor effect on model outcomes (appendix). Only very high and relatively unrealistic mutation rates (1×10^{-2}) produced alterations in diversity-migration relationships. In those cases, mutation enhanced maladaptation and reinforced overall patterns elicited by maladaptation.

Discussion

Simulation Outcomes

The movement of genes and individuals across a selective gradient provides a number of important evolutionary-demographic feedbacks that can contribute to our understanding of species diversity (Kawecki et al. 1997; Ronce and Kirkpatrick 2001; Holt 2003). Yet ecologists have only begun to understand the manifold links between genetic and species diversity (Vellend and Geber 2005). The models explored here provide an initial step toward disentangling how joint evolutionary and ecological dynamics determine multispecies coexistence in mass-effects metacommunities. As genetically diverse populations become distributed across a heterogeneous landscape, selection can become relatively inefficient in sink habitats, which can produce maladaptation (Holt and Gomulkiewicz 1997; Kawecki et al. 1997; Ronce and Kirkpatrick 2001; Thompson et al. 2002; Holt 2003). Maladaptation can reinforce population asymmetries that tend to lower fitness in sink habitats even further (Ronce and Kirkpatrick 2001). These demographic effects, at least in principle, could enhance species coexistence if competition is structured as a zero-sum game. However, this outcome is not a foregone con-

clusion, because maladaptation also produces dramatic asymmetries between source and sink population abundances that could preclude coexistence if fit populations preempt shared resources.

In the simulations presented, sink-source dynamics played an important role in shaping the outcome of evolution. Asymmetric migration and gene flow induced pervasive maladaptation in sink populations. Only populations inhabiting patches supporting their highest regional fitness became locally adapted. Source populations were also relatively abundant relative to coexisting populations and thus provided a substantial source of maladapted immigrants into other patches. In general, results agree with those of Amarasekare (2000), who predicted that sink-source (mass-effects) dynamics would generate a few highly abundant species or genotypes in some parts of the landscape, many small sink populations in other areas, and a general diminishment of both genetic and species diversity with community isolation. At the same time, explicitly linking species and genetic diversity in this simulation created novel outcomes different from those generated without fitness linkages between the two forms of diversity.

In many cases, maladaptation is considered a disruptive force in the persistence of species (Ronce and Kirkpatrick 2001). However, I show here that this need not be the case. Simulations suggest that pervasive maladaptation across a landscape can maintain species richness when communities are linked by sufficient interpatch migration and competition is structured as a zero-sum game. In this way, community context plays an important role in shaping how maladaptation influences the outcome of species interactions. The demographic effects of maladaptation produced novel predictions for species richness in two regions of proportional migration. In the low-migration region, evolution significantly reduced local species richness. In the region of intermediate migration, evolution enhanced local species richness. Perhaps most surprising, maladaptation supported local and regional coexistence of all species in the regional pool under a broad range of intermediate levels of migration. Although qualitative patterns of unimodal species richness relative to migration proportion were robust to maladaptation, this outcome is predetermined by intrinsic boundary conditions placed by

Figure 4: Mean relative maladaptation (*top*), reproductive rate (*middle*), and relative abundance (*bottom*) for each species within a patch organized by rank abundance. Results for 10%, 30%, and 50% proportional migration were obtained by 25 runs of the mass-effects metacommunity with (*circles*) and without (*squares*) evolution after early community assembly ($\Delta t = 20$ generations). The gray line in the relative abundance plot indicates assumed extinction threshold at 0.01. Species ranks with relative abundances that fell below this value were assumed extinct. Error bars indicate standard deviations; absence of error bars indicates that standard deviations fell within symbol extents. The evolutionary model was analyzed with δ set to 0.10.

low and high proportional migration on spatial fitness variance (Mouquet et al. 2005).

The divergent community outcomes resulting from metacommunity evolution derived from the differential action of two demographic outcomes of maladaptation over a gradient of migration propensity. With migration, maladaptation substantially decreased reproductive rates in subordinate competitors, while source populations evolved to maximum potential reproductive rates close to their optima. This maladaptation elevated population asymmetries between patch-competitive dominants and subordinates, which, in turn, shifted subordinate-competitor abundances below the extinction threshold when migration was sufficiently low. At the same time, maladaptation enforced a greater absolute decline in reproductive rates of intermediate-ranked competitors. This effect produced a greater similarity in reproductive rates among subordinates (fig. 4). At intermediate migration, a greater similarity in the reproductive rates among subordinates allowed for persistence of the poorest competitors in each patch, given that coexistence is a zero-sum game. This leveling effect of maladaptation suggests a novel evolutionary-ecological mechanism of species coexistence, in which proportionate fitness declines among phenotypes create a local trade-off between a species' maximum potential fitness in a patch and its absolute fitness decline through maladaptation. It relies on a divergence in the scaling between ecological and evolutionary mechanisms of fitness determination. Such differences provide an important means by which ecological predictions can differ when perturbed by evolutionary change (Urban and Skelly 2006).

Model Assumptions and Caveats

I made a number of simplifying assumptions about the ecological and evolutionary processes underlying model dynamics. The divergence between evolutionary and mass-effects metacommunity models depended on the assumption that individuals experienced lower proportional fitness after emigration into heterogeneous environments. When no phenotypic trade-offs were assumed, evolution did not alter predictions. This outcome suggests that a more complex evolving metacommunity perspective may be needed when strong fitness trade-offs characterize phenotypic responses to heterogeneous selection. However, simpler nongenetic models may be appropriate for systems dominated by weak or nonexistent interpatch phenotypic trade-offs. The phenotypic trade-off assumed here describes a constraint on multitrait adaptation that operates in a landscape mosaic of antagonistic selection (Crespi 2000; Lenormand 2002; Thompson et al. 2002). Such mo-

saics of antagonistic selection often describe natural landscapes (Thompson 2005).

I also assumed a simple phenotypic model for the evolution of asexual haploid clones. Although the process of phenotypic evolution assumed in the simulation omits more complex genetic architectures, such as correlated multigene selection, epistasis, and sexual recombination, the model provides a reasonable compromise between biological realism and computational complexity. Sexual recombination, in particular, could have important effects on local coexistence, given its potential to maintain genetic diversity (Vellend 2005). The effect of complex genetic architectures on diversity patterns remains a subject of ongoing study. I assumed that species shared the same level of proportional migration and that migration propensity did not evolve. Previous research suggests that variable migration abilities among hosts and parasites can alter their joint coexistence (Gandon et al. 1996; Thrall and Burdon 1999; Gandon 2002). Future models should evaluate the effect of heterogeneous migration rates on multispecies evolutionary model outcomes. The evolution of dispersal creates another layer of complexity that could generate significant departures from model outcomes. In the absence of temporal heterogeneity, selection generally favors the evolution of low dispersal from stable sinks into sources (McPeek and Holt 1992; Holt 1993). Thus, allowing migration to evolve could move the system under study toward low local species richness as each species becomes restricted to its optimal habitat.

Applying Model Outcomes

Three lines of evidence suggest that model results should apply to a wide range of natural systems. First, maladaptation via gene flow is a common feature of natural populations that receive migrants from divergent environments (Lively 1999; Crespi 2000; Thompson et al. 2002). The range of potential maladaptation explored in our simulations was consistent with biologically realistic values. Among 14 recently (2000–2004) published examples of interaction traits, the maximum relative decline in measured fitness components varied from 13% to 95% when divergent phenotypes were expressed in antagonistic communities (M. C. Urban and D. K. Skelly, unpublished data). Second, trade-offs between traits that facilitate fitness in divergent environments frequently characterize the genetic structure of natural populations (Lenormand 2002; Kawecki and Ebert 2004; Strauss and Irwin 2004). It is unknown when selection on reproductive rates between and within species will differ in proportionate and absolute effects on fitness across environmental gradients. However, strong evidence points to the importance of proportionate fitness declines that limit the success of divergent phe-

notypes to specific selection regimes (Zangerl and Berenbaum 2003; Hendry and Taylor 2004; Nosil 2004). Phenotypic trade-offs often promote microgeographic adaptations of populations to local conditions despite moderate gene flow (Kawecki and Ebert 2004; Skelly 2004; Urban and Skelly 2006). Third, the same landscape structure that generates local maladaptation and evolutionary trade-offs, namely, interpatch connectivity and heterogeneity, characterizes the landscape structure assumed by niche-based metacommunity theories (Amarasekare and Nisbet 2001; Chase and Leibold 2002; Mouquet and Loreau 2002). These assumptions find support in empirical studies of natural metacommunities (Cottenie et al. 2003; Urban 2004; Thompson 2005). Hence, evolutionary trade-offs and ensuing maladaptation may characterize many of the interacting populations assembled into metacommunities.

Simulation results make the testable prediction that a competitive metacommunity consisting of genetically variable species will have greater local diversity at intermediate proportional migration when compared to a metacommunity with low genetic variance within species. The opposite should be true when low (~10%) proportional migration is assumed. I am not aware of experimental evidence available to test these predictions. However, I hope that analyses will encourage research in this area. The emergence of novel experimental approaches that combine manipulations of gene flow (Forde et al. 2004) and of the genetic composition of interacting populations (Booth and Grime 2003) provides an exciting means to test evolutionary-ecological predictions in model metacommunities.

Metacommunity Ecology and Evolution

Simulations presented here bridge the gap between multispecies metacommunity models of coexistence without evolution (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002; Mouquet et al. 2005) and those of single-species sink-source evolution (Kirkpatrick and Barton 1997; Ronce and Kirkpatrick 2001; Kawecki and Holt 2002). Mass-effects metacommunity models generally predict the greatest local species richness where moderate immigration restores species lost because of local interactions but migration is not so great as to synchronize competition at regional scales (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002; Mouquet et al. 2005). Sink-source models of adaptation generally predict that maladaptation will dominate in sink habitats unless migration is very low and that this maladaptation can feed back on population asymmetries and further extend fitness declines (Ronce and Kirkpatrick 2001; Kawecki and Holt 2002). In a single-species model, high movement was expected to frustrate

local adaptation and decrease the persistence of species (Ronce and Kirkpatrick 2001). However, the model presented here shows that scaling up the demographic outcomes of maladaptation to a multispecies context will depend critically on the assumed form and strength of local interactions. In this research, the zero-sum game assumed to characterize indirect competitive interactions for a limited resource and regional similarity in species fitnesses created a situation where a local fitness trade-off leveled asymmetries in local competitive abilities and promoted local species richness. Thus, the particular form and type of interspecific interactions in a community can either buffer or enhance the negative consequences of maladaptation on species coexistence.

A growing body of evidence indicates the importance of a community approach to understanding how evolution molds ecological outcomes (Case et al. 2005). Models of pairwise coevolution in homogeneous and spatially subdivided landscapes illustrate that spatial refuges can maintain the genetic variation needed to respond to dynamic and reciprocal selection from interacting species (Gandon et al. 1996; Antonovics et al. 1997; Lively 1999; Gomulkiewicz et al. 2000; Gandon 2002). In heterogeneous landscapes, a similar effect is produced such that migration expands the range of patches invaded by predator and prey genotypes (Hochberg and van Baalen 1998). In this model, maladapted populations were maintained in sink habitats via dispersal from source habitats in a manner similar to the operation of sink-source dynamics in this study. Two recent models (Vellend 2005, 2006) extend knowledge generated by pairwise interaction models to multispecies metacommunities. In a competitive metacommunity, assuming heterogeneous patches and differing species and phenotypic optima, Vellend (2005) found that species richness increased with migration rate (ranging from 0.001 to 0.1), an outcome that is generally consistent with results presented here. In another evolving metacommunity model that assumed coevolutionary interactions among competing species, species richness was maintained at higher levels when genetic diversity and potential genotypic range were expanded (Vellend 2006). Thus, work on evolution in multispecies metacommunities supports a growing recognition that evolution can promote species richness under varying assumptions about the species pool, fitness trade-offs among habitats, and migration.

Conclusions and Future Directions

The coexistence of multiple species within mosaic environments has been attributed to both ecological (Hutchinson 1959; Chase and Leibold 2003) and evolutionary mechanisms (Gandon et al. 1996; Lively 1999; Thompson 1999; Nuismer et al. 2000). Our knowledge about the dy-

namics of traits in pairwise interactions (reviewed by Thompson [2005]) and community composition and diversity in metacommunities (reviewed by Leibold et al. [2004]; Holyoak et al. [2005]) has increased significantly in recent years. Yet we still know relatively little about evolution's effect on the emergent properties of multispecies metacommunities. To date, metacommunity theory has generally ignored the consequences of evolution for predictions about the structure and dynamics of linked communities (but see Hubbell 2001; Leibold et al. 2005; Urban and Skelly 2006). If simple phenotypic trade-offs among patches can alter patterns of species richness substantially from those ignoring genetics, as shown here, then metacommunity models often may produce inaccurate predictions. Hence, as empirical research increasingly is brought to bear on metacommunity theories, successful prediction may be limited without an evolutionary perspective (Vellend 2005, 2006; Urban and Skelly 2006). An evolving metacommunity perspective, on the other hand, assumes that population demography and genetic structure are strongly dependent on regional dispersal and that communities are characterized by multiple species linked by diffuse and indirect interactions (Urban and Skelly 2006). This perspective argues for deeper inspection of the basic biological mechanisms that determine the outcome of species interactions and the maintenance of genetic and species diversity over spatial gradients. Such investigations are likely to uncover many ecological-evolutionary mechanisms that alter species diversity and other emergent community properties that would not be predicted under a purely ecological framework.

Acknowledgments

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