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# Evolution in Metacommunities: On the Relative Importance of Species Sorting and Monopolization in Structuring Communities

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**ABSTRACT:** Adaptive evolution within species and community assembly involving multiple species are both affected by dispersal and spatiotemporal environmental variation and may thus interact with each other. We examined this interaction in a simple three-patch metacommunity and found that these two processes produce very different associations between species composition and local environment. In most conditions, we find a pattern we call "species sorting," wherein local adaptation by resident species cannot prevent invasions by other preadapted species as environmental conditions change (strong association between local environmental conditions and local community composition). When dispersal rates are very low relative to the other two rates, local adaptation by resident species predominates, leading to strong priority effects that prevent successful colonization by other species that would have been well adapted, a pattern we call "local monopolization." When dispersal and evolutionary rates are both very high, we find that an evolving species outcompetes other species in all patches, a pattern we call "global monopolization." When environmental oscillations are very frequent, local monopolization predominates. Our findings indicate that there can be strong modification of community assembly by local adaptive processes and that these depend strongly on the relative rates of evolution, dispersal, and environmental change.

**Keywords:** evolutionary metacommunity, species sorting process, monopolization hypothesis, environmental fluctuations.

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Recent theoretical developments in both evolutionary ecology (e.g., Thompson 1997, 1999a, 1999b, 2005; Hanski and Gaggiotti 2004) and community ecology (e.g., Leibold et al. 2004; Holyoak et al. 2005) emphasize the possibly strong role of dispersal among local populations and communities in regulating the distribution of genetic variability and species distributions at regional and local scales. This recent work builds on earlier work (e.g., Wright 1969; Levins and Culver 1971; Hastings 1980) but seeks a new level of understanding about how spatial and evolutionary ecology affect species interactions. Additionally, recent reviews show that microevolutionary processes of adaptation frequently occur on very fast timescales (e.g., Kingsolver et al. 2001; Kinnison and Hendry 2001) similar to those involving ecological processes in population dynamics or community change (Hairston et al. 2005; Urban and Skelly 2006). The possible equal timescale of evolution and ecology and the common influence of dispersal suggest that the two processes may interact in important ways to affect spatial evolutionary ecology.

However, to date, work on this interaction is very limited. On the one hand, evolutionary models of spatial adaptation and coadaptation (reviewed in Thompson 2005) have increasingly sought to explain how species interactions affect population genetic divergence patterns. They have, however, largely ignored consequent effects and feedback on ecological patterns of coexistence, diversity, and food web structure. On the other hand, metacommunity models (reviewed in Leibold et al. 2004) have increasingly found that dispersal can strongly alter community assembly either by the effects of dispersal limitation on community assembly or by the consequences of source-sink relations in local populations. Metacommunity models have, however, ignored how dispersal affects patterns of evolution of component species. Work on this interaction of ecological and evolutionary processes in metacommunities is limited (Hochberg and van Baalen 1998; Nuismer and Kirkpatrick 2003; Morgan et al. 2005), and none of the articles has addressed how evolution and com-

munity assembly may interfere with each other in affecting how species are distributed among habitats. Here we use a very simplified model to investigate such possible interference. The simplicity of our scenario allows us to understand the resulting dynamics and interpret them mechanistically and can thus serve as a baseline model for future work on this topic.

We are particularly interested in evaluating how adaptive evolution may alter our current expectation of metacommunity dynamics. Work to date on metacommunity dynamics has identified four paradigms that inform our understanding of community assembly (though these are not mutually exclusive; Ellis et al. 2006). One of these, the neutral view (Hubbell 2001), views all individuals of all species as equivalent in all environments. Under this view, drift dynamics are important in community assembly. Its strong connection to neutral evolution models is obvious. The other three paradigms view community assembly occurring under different scenarios. In the patch dynamics view, dispersal occurs on a timescale that is distinctly longer than that of local ecological dynamics. This creates situations in which community species composition tracks only local environmental change, with a distinct lag, allowing for a number of possible dynamics, including colonization-competition trade-offs and mismatches between local community composition and environmental conditions. In the species-sorting view, colonization serves as continuous low-level input that overcomes such lags in compositional tracking of local environment by the community. Dispersal is assumed to have no other effect on local population dynamics. If this is combined with the assumption that populations rapidly approach near-equilibrium behavior, it results in a maximal level of correspondence between species composition of the community and the local environment. Finally, the mass effects perspective assumes that dispersal is strong enough to permit strong source-sink relations among populations from different local populations. This can disrupt tracking of local environmental conditions by community composition because regional influences on local composition become stronger than local effects. Thus, dispersal has important effects that influence the degree to which local community assembly can track local environmental conditions that are optimized at some intermediate level (Chase and Leibold 2003; Leibold and Norberg 2004). It is unknown to what degree these paradigms are influenced by local adaptation of resident species, and it is this question we seek to evaluate in this article.

To visualize our model, consider a set of local patches that are connected to each other by some level of dispersal. These patches differ in local environmental conditions so that different ecological traits are favored in space and time. At present, models of adaptive dynamics emphasize

the role that adaptive evolutionary change in local populations plays in determining how closely changes in the trait distribution of these populations may follow or track such environmental change. These models identify two important roles for dispersal. On the one hand, gene flow shows its importance by constraining the degree to which local populations can adapt to local conditions and thus track local environmental fluctuations. Alternatively, gene flow can also be important in maintaining genetic variation, on which local selection can act, and this may be particularly important in allowing populations to respond to local changes in selection if there is gene flow from other communities where such adaptation has already occurred.

Current models of community assembly under conditions with similar variation in time and space in local conditions emphasize how context-specific species interactions will be affected by environmental change and how this may favor different species in different patches and may allow species composition to change in response to local environmental change. Again, dispersal plays an important role in determining either how much time may occur before compositional change responds to local environmental change (Chase and Leibold 2003; Leibold and Norberg 2004) or the importance of sink populations (maintained by dispersal from other patches) that affect local species interactions (Amarasekare and Nisbet 2001; Mouquet and Loreau 2003).

Under a scenario resembling this situation, De Meester et al. (2002) suggested that community assembly might not always be as important as adaptation. They argue that rapid local adaptation can allow early colonists or resident species to track environmental change sufficiently fast so as to alter patterns of community assembly. They also argue that such rapid local adaptation can work even when there is high dispersal, such as seems to be the case in zooplankton communities (and other pond assemblages). Thus, strong priority effects may result in weakened correlations between the species composition and local environmental conditions of local communities. This occurs because there are strong correlations between the genetically determined ecotypes of species and local conditions instead.

### Presentation of the Model

Our goal is to illustrate this interaction between local adaptation and community assembly in a simple but illustrative case. It is likely that more complex scenarios will produce somewhat different outcomes, and we evaluate some possibilities in the appendix in the online edition of the *American Naturalist*. Our case shows an interaction between adaptation and community assembly that qual-

itatively illustrates many features likely to occur in more complex and/or realistic cases.

We assume that the metacommunity consists of three patches connected by dispersal that may vary in rate. The different patches  $j$  are characterized by a single environmental metric  $e_j$  that is assumed to be constant in the first two patches ( $e_1 = -0.5$ ,  $e_2 = 0.5$ ) but fluctuates periodically in the third patch ( $e_3 = \sin(2\pi t/p)$ , where  $p$  is the period of the fluctuations and  $t$  is time). These environmental metrics could be thought of as any characteristics of the environment affecting the fitness of the individuals in the metacommunity (e.g., temperature, pH, redox potential). These assumptions are summarized in figure 1 and result in the maintenance of both spatial and temporal variation in local environmental conditions in the metacommunity.

Each species (denoted by the subscript  $i$ ) of the metacommunity is characterized by its trait  $x_i$ . For each trait  $x_i$ , we define the fitness  $f(x_i, e_j)$  of individual  $i$  in patch  $j$  by

$$f(x_i, e_j) = \frac{f_0}{\sqrt{2\pi}\sigma} \exp\left[-\frac{(x_i - e_j)^2}{\sigma^2}\right]$$

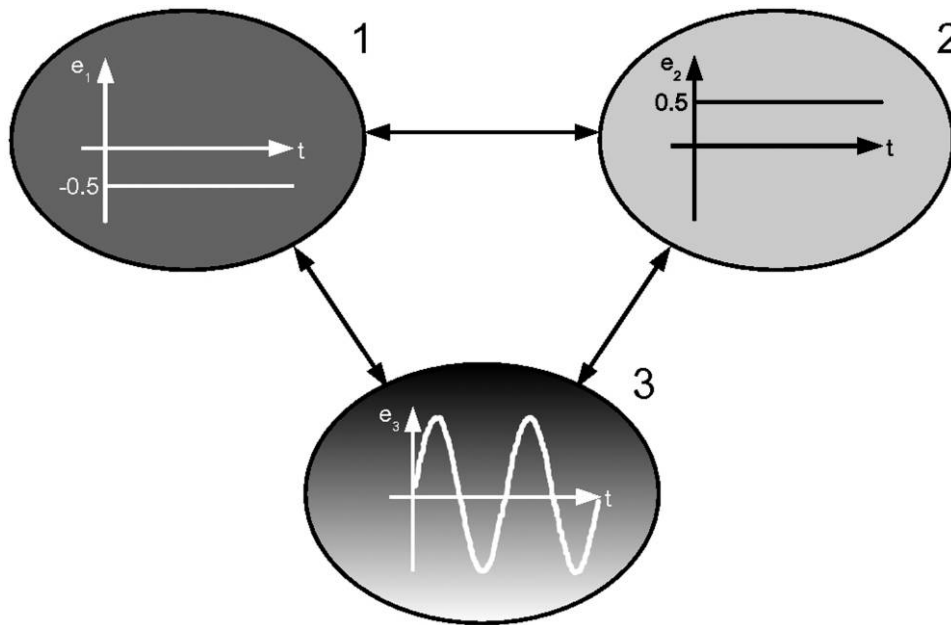
so that fitness is maximum when the trait value  $x_i$  matches the metric of the environment  $e_j$ .

Because the model considers evolution, dispersal, and

temporal variations, direct mathematical analysis is difficult, and we use simulations to evaluate the resulting dynamics. At the beginning of the simulations, there are three species in the metacommunity. The first two species are perfectly adapted to the constant environment of patches 1 and 2:  $x_1 = -0.5$  and  $x_2 = 0.5$ . We assume that these two species do not further evolve during the rest of the simulations. The third species is initially perfectly adapted to the environment of the third patch ( $x_3 = 0$ ), but its fitness then varies through time because of fluctuations in the environmental trait of the third patch. Contrary to the two other species, we assume that species 3 evolves by successive mutation and selection events, thereby giving birth to new genotypic morphs  $x_k$  ( $k > 3$ ).

We assume that at  $t = 0$ , all three species fill the patch to which they are adapted. Each of the patches  $j$  contains a number of microsites  $N_j$ , and each of the microsites may contain only one individual of any species. The total number of microsites of the patch  $j$  occupied by species  $x_i$  is denoted  $N_{i,j}$ . At the beginning of each time step, all microsites of a given patch are occupied, so that  $\sum_{i=1}^s N_{i,j} = N_j$ , where  $s$  is the total number of morphs (species plus genotypic morphs of species 3) present in the metacommunity at that time. At first we assume that the number of microsites is the same in all patches so that  $N_j = N$ ,  $j \in \{1, 2, 3\}$ . We discuss deviations from this hypothesis in the appendix.

The dispersal rate  $d$  is the probability that an individual



**Figure 1:** Presentation of the metacommunity. For all three patches, the level of gray indicates the value of the environmental trait. This value and its variations through time are displayed by the graphs in each of the three patches.

disperses from a local community at each time step, so the expected number of dispersers of morph  $x_i$  leaving patch  $j$  is  $dN_{i,j}$ . Each disperser has a probability  $m_d$  of dying while dispersing, so after mortality, the expected number of dispersers is  $(1 - m_d)dN_{i,j}$ . The dispersers are then divided equally between the two other patches of the metacommunity.

After dispersal, we assume that all individuals of the metacommunity have an identical probability of dying (intrinsic mortality  $m$ ). Because of this intrinsic mortality and the death involved in the dispersal process, the three patches of the metacommunities are no longer saturated. For a given patch  $j$ , we denote the number of empty microsites by  $V_j$ . The expected value of  $V_j$  is  $E(V_j) = N[dm_d + m(1 - dm_d)]$ . The empty microsites are then filled by reproduction of the individuals of different species and genotypic morphotypes present in the local patch. The probability of an empty microsite being filled by an individual of morph  $i$  is proportional to the relative individual fitness of this morph,  $f(x_i, e_j)$ , multiplied by the number of microsites occupied by this morph,  $N'_{i,j}$ , after the dispersal and mortality events. Therefore, the total recruitment  $r_{i,j}$  of morph  $i$  in patch  $j$  is expected to be

$$r_{i,j} = V_j \frac{f(x_i, e_j)N'_{i,j}}{\sum_{k=1}^s f(x_k, e_j)N'_{k,j}}.$$

If a microsite is filled by an offspring of the third species ( $i \geq 3$ ), a mutation may occur with a probability  $\mu$ . If a mutation occurs, the microsite is filled with a morph whose trait is drawn randomly from the interval  $[x_i - a, x_i + a]$ , where  $x_i$  is the trait of the parent of the mutant. After this mutant appears in the population, it may outcompete the resident population if it is better adapted to its environment. Note, however, that it may also disappear because the mutant is introduced as a single individual and may fail to invade, even if its fitness is higher than that of the resident, because of demographic stochasticity (intrinsic and dispersal mortality being drawn at random).

The different events in a given time step are summarized in figure 2. Note that at the end of the reproduction event, the patch is saturated, and the next time step can begin. We want to stress here that the selection process operates only during the reproduction step, with the other events of the time steps being of the neutral type, in the sense that the probability of their occurrence is independent of the trait of the individual. We do not expect the results to change if selection acts on intrinsic mortality  $m$  instead of reproduction.

The variables and parameters of the model are summarized in table 1. The default values of the parameters

are also indicated. We consider variations in the three timescales of model: the dispersal timescale dynamics, defined by the rate of dispersal  $d$  (from  $10^{-9}$  to 1); the evolutionary timescale, defined by the mutation probability ( $10^{-5}$  to  $10^{-3}$ ); and the characteristic timescale of the local environmental fluctuations, that is, the period  $p$  of the oscillations of  $e_3$  (from three time steps to 300,000).

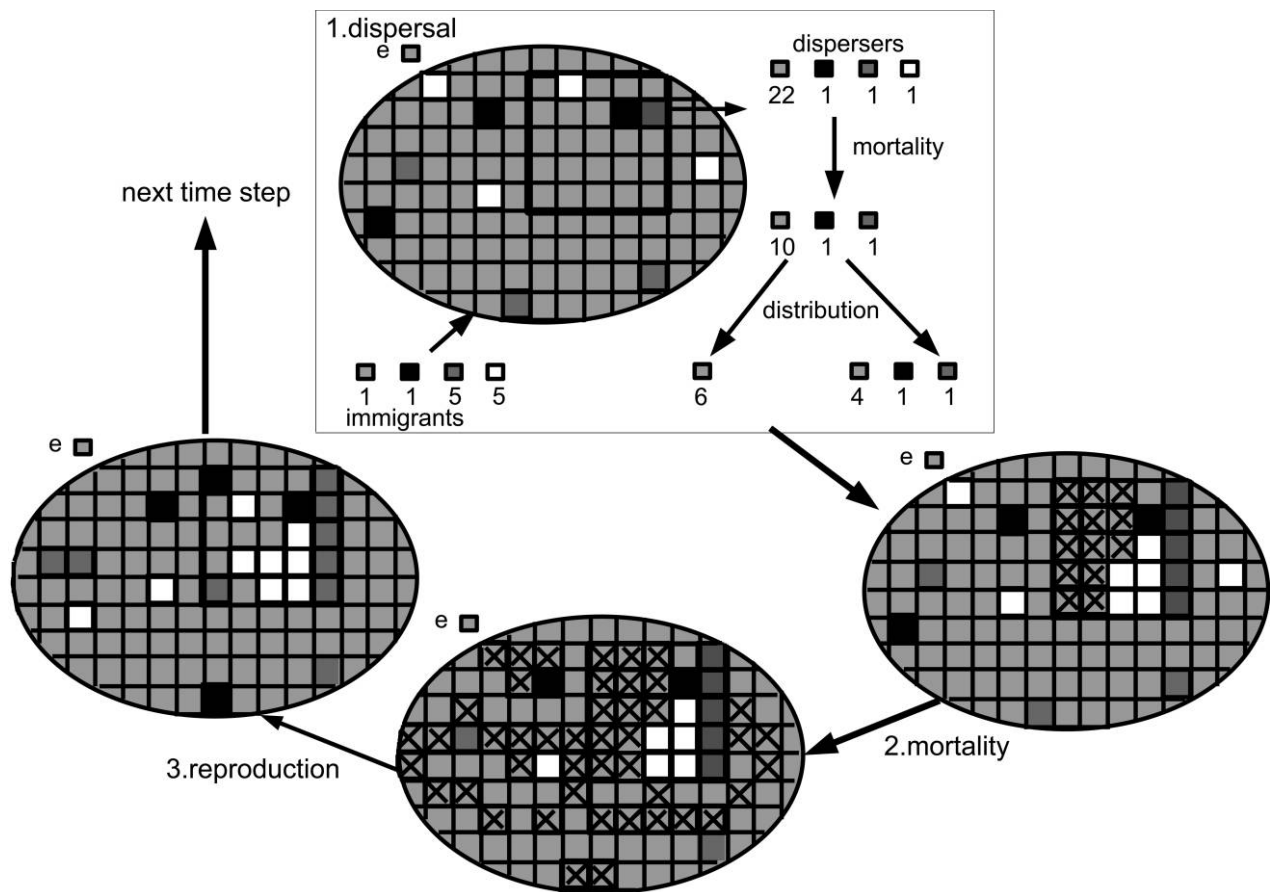
The assumptions of the species-sorting paradigm and the monopolization hypothesis indicate that these three timescales are likely to strongly alter how species sorting and local adaptation interact to structure the metacommunity. In the appendix, we focus on these three factors in evaluating our model and determine how robust they are to other factors, including heterogeneity in dispersal rates among the species, heterogeneity in patch size (i.e., number of microsites) among patches, presence of more than three species, and existence of more than three patches.

## Results

At the beginning of the simulation, the environmental trait in patch 3 is  $e_3 = \sin(0) = 0$ , and species 3 (initiated with a trait value of 0 as well) is therefore perfectly adapted to this patch. To set a baseline, we start with the assumption that species 3 does not evolve. As  $e_3$  increases, species 3 becomes less and less adapted to the local conditions in patch 3. As  $e_3$  changes and approaches 0.5, species 2, with trait  $x_2 = 0.5$ , becomes better adapted to the environment of patch 3 and is eventually better adapted to it than is species 3. At this point, it will be able to invade patch 3 of the metacommunity and will drive species 3 to extinction. During the rest of the simulation, the relative proportion of the species  $x_1$  and  $x_2$  will vary through time, along with the environmental fluctuations of  $e_3$ . Therefore, when there is no evolution or when evolution is extremely slow, a rapid species-sorting process takes place, and species 3 becomes extinct, while the other two species reciprocally invade patch 3 as the environment fluctuates to their advantage. This outcome occurred in all of our simulations over the range of parameters we studied when the mutation rate was 0. This result is consistent with current thinking in metacommunity ecology, where the role of adaptive evolution within species is ignored.

We examined the effects of variations of the three timescales previously described (dispersal, evolution, and environmental fluctuations) to evaluate how robust this species-sorting process is when species 3 can evolve. We found that there were three qualitatively distinct outcomes, as illustrated in figure 3. Figure 3A displays what happens when the level of dispersal is high and the period of the environmental fluctuations and the evolution speeds are intermediate. In this case, even though species 3 may





**Figure 2:** Decomposition of the events happening in a given patch during one time step. The environmental trait of the patch is given by the shaded box next to  $e$ . The squares of the patch are filled by an individual whose trait is indicated by the gray level, except when there is a cross in the microsite (empty microsite). Although the morphs are distributed in the patch displayed here, we do not keep track of the spatial distribution of morphs within patches in the model. For the dispersal phase, numbers below the squares correspond to the number of individuals of the given type that disperse.

evolve, species 2 is still able to invade the fluctuating patch, and the species-sorting process described above takes place. Species 3 is excluded from the metacommunity, and the abundances of species 1 and 2 in the metacommunity fluctuate through time, as is the case when species 3 cannot evolve. This result is the most frequent outcome of the simulations in the range of parameter values for dispersal, mutation, and environmental periodicity we modeled. This means that although species 3 can evolve and adapt to the local conditions, the exclusion by better-adapted immigrant species in response to environmental change is still possible and, in the range of conditions we modeled, very likely. In our model, as patch 3 becomes environmentally similar to patch 2, species 2 is sufficiently well adapted to patch 3 that it can exclude species 3, even though species 3 is adapting to this change (with some lag). Here species 2 has the added advantage of being

temporally better adapted to patch 3 than is species 3 and of having immigration of such adapted types into patch 3 that further inhibits population growth of species 3 via mass effects.

In contrast, when dispersal is very small (fig. 3B), the evolving species (species 3) is able to survive in patch 3. Because of the low dispersal probability, species  $x_1$  and  $x_2$  are not likely to migrate into patch 3 at a time when the environment could be favorable for them. Even if they were to migrate into patch 3 and if their migration is timely, migration is too weak to meaningfully inhibit species 3 via mass effects, as it was in figure 3A. Any population that does become established, therefore, becomes extinct because of demographic stochasticity. As the environment continues to change, species 3 then competitively excludes species 2, and as it changes further so as to resemble patch 1, species 3 again can adapt to this

**Table 1:** Presentation of the variables and parameters of the model: significance, units, and default value

Variables and parameters	Description (default value)
$s$	Total number of morphs
$x_p, i \in \{3, 4, \dots, s\}$	Characteristic trait of the morphs of the evolving species
$N_{i,p}, i \in \{1, 2, \dots, s\}, j \in \{1, 2, 3\}$	Number of microsites occupied by individuals of the morph $x_i$ in the patch $j$
$N_p, j \in \{1, 2, 3\}$	Number of microsites in the patch $j$ (100,000)
$m_d$	Probability of a dispersing individual's death during the dispersal event (0.5)
$m$	Intrinsic probability of a given individual's death during a time step (0.2)
$a$	Maximum amplitude of mutation (0.05)
$\mu$	Probability of mutation per offspring ( $10^{-3}, 10^{-4}, 10^{-5}$ )
$d$	Probability of a given individual's dispersal during a time step ( $10^{-q}, q \in \{0, 1, \dots, 9\}$ )
$p$	Period of the environmental fluctuations (3, 30, 300, 3,000, 30,000, 300,000)
$\sigma$	Variance of the fitness function, tolerance of the individual to different environments (0.1)
$f_0$	Parameter determining the maximum fitness (1)

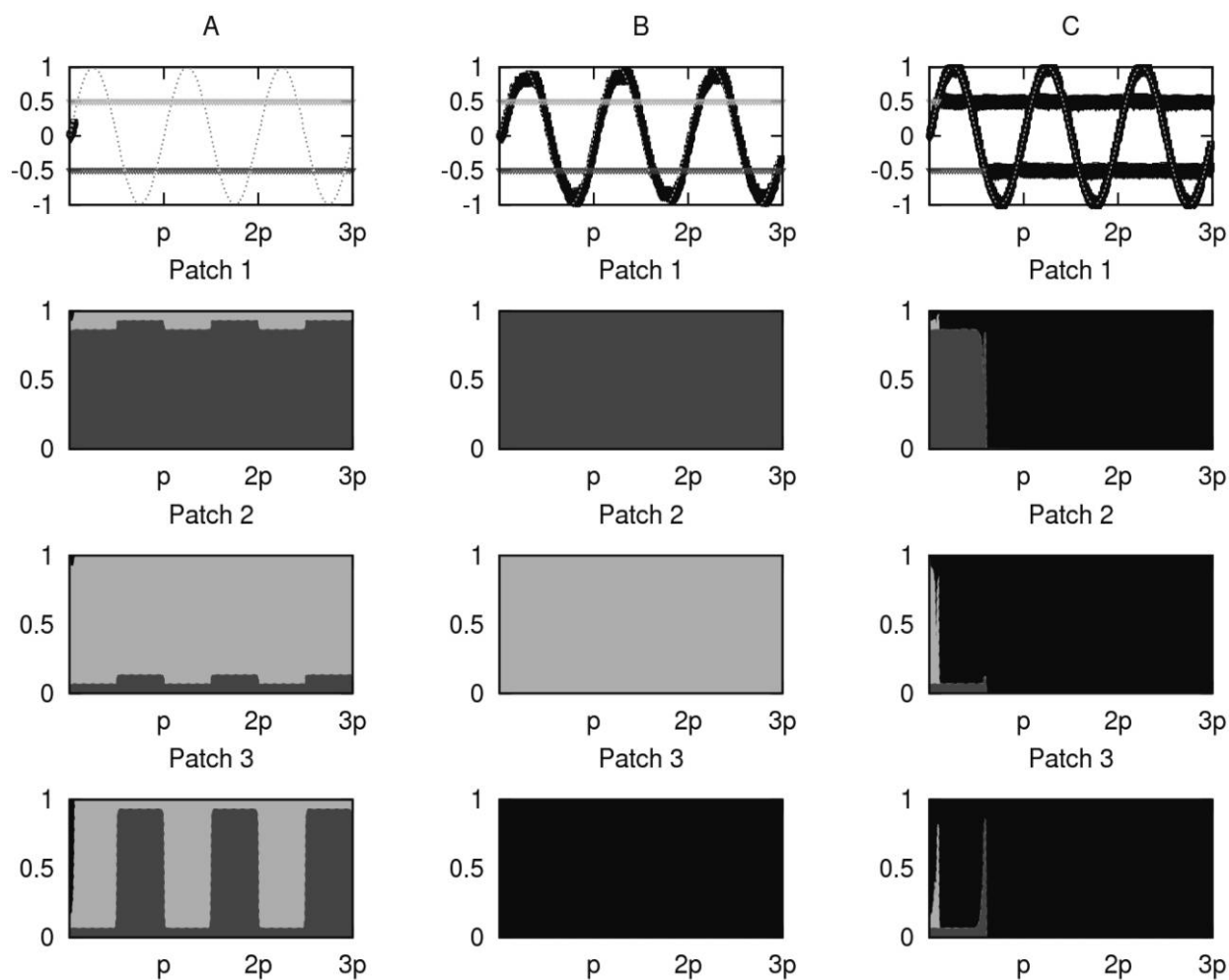
change and similarly prevent invasions by species 1. Thus, each species continues to monopolize the patch in which it was first found, despite environmental fluctuations. If dispersal is low enough, such local monopolization may occur even if species 3 adapts relatively slowly (because it has a low mutation rate) so that it is rarely near the optimum trait value for the environment. In the rest of the article, we refer to such a situation as “local monopolization” because the evolution of species 3 allows it to escape the species-sorting process, even when such evolution is not fast enough for the species to perfectly track the environmental fluctuations. Under these conditions, there is less correspondence between local environmental conditions and species composition than there was in the case described in figure 3A.

Figure 3C shows the result of a simulation in which the rate of dispersal is high and evolution is fast (high mutation rate). In such cases, we find that species 3 not only is able to maintain itself in the fluctuating patch 3 but also invades the rest of the metacommunity. As the environment in patch 3 approaches that of patch 2 ( $e_3$  approaches 0.5), species 3 can compete with species 2 in patch 2 and become competitively equivalent to it. It has an additional advantage due to migrants from patch 3 that can exist in patch 2 as sink populations even when  $x_3$  is not exactly equal to 0.5. These sink populations can then also evolve and provide a further advantage to species 3 over species 2. It is this combination of being equally adapted to patch 2 as species 2 and the additional effect of migrants from patch 3 that gives species 3 the advantage needed to exclude species 2 from patch 2, even though species 2 is also optimally adapted to patch 2. Species 2 also has sink populations in patch 3, but these individuals rapidly become maladapted to patch 3 as it continues to change and there is little long-term impact on species 3 in patch 3. In this simulation, species 3 then excludes species 1 from patch 1 via the same mechanism when the environment of patch 3 approaches that of patch 1. We refer to this situation as

“global monopolization.” The result is a single species that closely tracks environmental conditions in all patches via local adaptation, and it can evolve despite the fact that the other species in the metacommunity are optimally adapted to their own set of patches.

When the oscillation frequency of the environment was very high (period  $< 300$ ), we found that local monopolization, where each of the three species (1–3) dominated each of the three patches (1–3), also occurred and that this was relatively independent of either the mutation rate or the dispersal rate. Here the environment changes at a rate that is shorter than the rate of competitive exclusion among the species, so any advantage of species 1 or 2 in patch 3 is too ephemeral to allow them to exclude species 3, and species 3 is able to remain in patch 3 because of its ability to have an average phenotype that is superior to theirs. Additionally, when the period is very small ( $= 3$  or 30), we found that species 3 evolved to be dimorphic (akin to sympatric speciation), with both morphs coexisting via temporal niche partitioning. Thus, at high frequencies of environmental fluctuations, all three species coexisted in the metacommunity via this process of local adaptation to each community. In the rest of the article, we focus our discussion on dynamics with slower environmental fluctuations where the tensions between local adaptation and species sorting are more relevant to metacommunity dynamics.

In addition to the three cases described above involving species sorting, local monopolization, and global monopolization, we found cases where species 3 was able to exclude one of the other two species from the metacommunity but not the third (fig. 4). The exclusion of the first species followed the scenario as described above for global monopolization, but species 3 was then unable to similarly exclude species 1 when the environment in patch 3 approached that of patch 1. This is because of the inhibitory effects of dispersal-mediated gene flow from patch 2, now monopolized by species 3, with trait  $x_3 = 0.5$ , which is

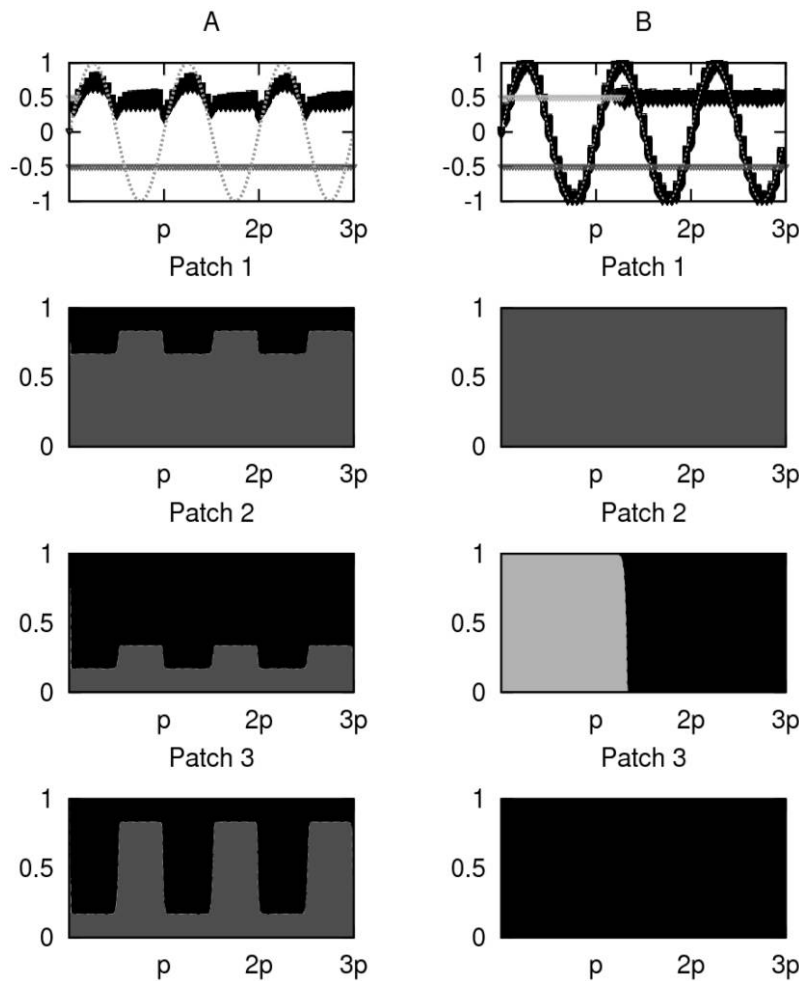


**Figure 3:** Three most common outcomes of the simulations. In *A* ( $p = 30,000$ ,  $d = 0.1$ ,  $\mu = 10^{-4}$ ), species sorting determines the structure of the metacommunity. Simulations leading to *B* differ from those leading to *A* in the dispersal rate ( $d = 10^{-9}$ ); the metacommunity is structured by local monopolization. Simulations leading to *C* differ from those leading to *A* in the period of the environmental fluctuations ( $p = 300,000$ ). *C* displays a global monopolization outcome. For each of the different columns, the first row corresponds to the values of the traits present in the metacommunity through time. Species 1 is dark gray, species 2 is light gray, and the evolving species 3 is black. Variations of the environmental trait are recalled (*dotted periodic curve*). The three other rows display the relative frequencies of the three species through time in patches 1 (second row), 2 (third row), and 3 (fourth row).

very poorly adapted to patch 1. When the evolutionary and dispersal rates are high, species 3 may invade patch 2 and replace species 2 but may be periodically excluded by species 1 in the fluctuating patch (fig. 4A). This case is then intermediate between global monopolization and species sorting. Alternatively, at low dispersal and medium to high mutation rates, the evolving species is still able to remain dominant in the fluctuating patch 3, so that the outcome is similar to a mix of global monopolization (in the sense that the evolving species invade patch 2 and exclude species 2) and local monopolization (fig. 4B). If

a favorable mutation appears at the right time (an event that is likely to happen in only some of the occasions when patch 3 resembles patch 2), the evolving species may invade the remaining patch of the metacommunity. Because of this, it is possible to see this kind of intermediate scenario as temporary and the global monopolization as the equilibrium state. Additional and longer simulations show that this nonequilibrium situation may have a long duration, and in some cases, we could not reach the global monopolization situation (results not shown). Therefore, these intermediate transient cases are arguably very likely





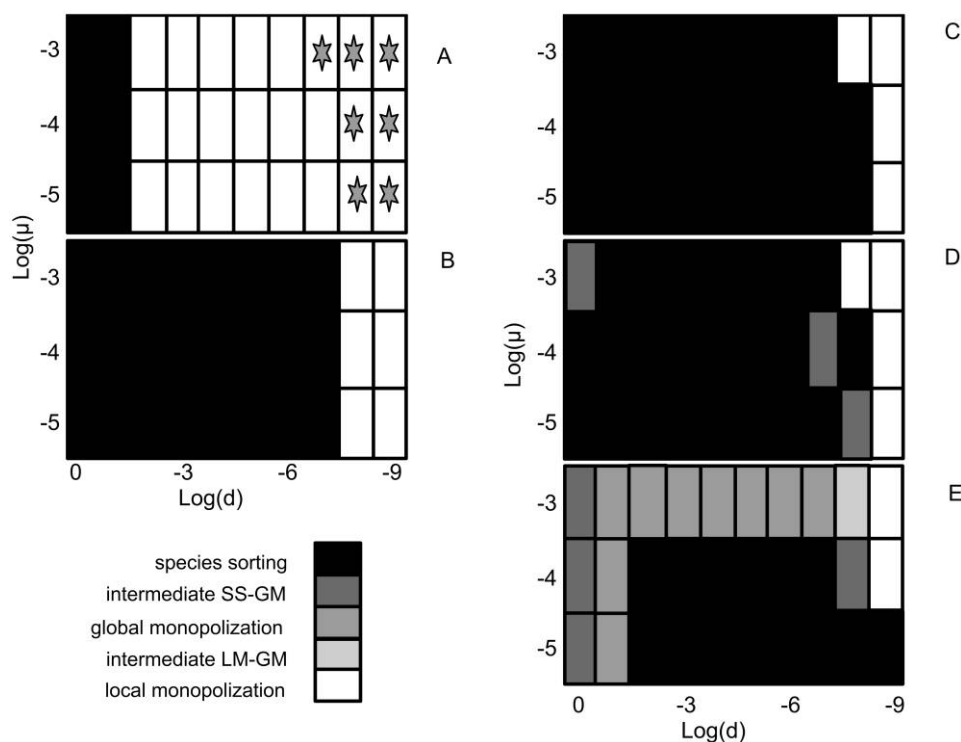
**Figure 4:** Some simulations whose outcomes are intermediate between the typical cases presented in figure 3. Column A ( $p = 300,000$ ,  $d = 1$ ,  $\mu = 10^{-5}$ ) presents an outcome that is intermediate between species sorting and global monopolization, while B ( $p = 300,000$ ,  $d = 10^{-9}$ ,  $\mu = 10^{-3}$ ) displays an outcome that is intermediate between local and global monopolization. Shaded areas and general organization of the figure are the same as in figure 3.

to be seen if one were to observe the metacommunity at a given time.

Figure 5 shows how the three different timescales (period of the oscillations, rate of dispersal, and mutation rate) determine when the species-sorting and monopolization hypotheses structure the metacommunity. Over the range of parameter space that we studied, we found that species sorting was the most common outcome. Even when environmental fluctuations are very slow (fig. 5E) and species 3 thus has more time to adapt to local environmental changes, species sorting is observed in almost half of the simulations. However, if dispersal is slow enough, local monopolization also occurs even when fluctuations are rapid. Local monopolization is less likely to

happen when fluctuations are slow (fig. 5E), as species 1 or 2 then has a wider time window to invade the fluctuating patch and may succeed in doing so in spite of the small amount of dispersal. Global monopolization requires slow changes of the environment (fig. 5E) and is more likely to happen when the mutation rate is high. It is the dominant outcome when the evolution speed is high and fluctuations are slow. Figure 5 also shows that the three idealized outcomes (species sorting, local monopolization, and global monopolization) are part of a continuum and are supplemented by intermediate mixed outcomes.

The figures we present here summarize the outcome of 180 simulations in which we systematically varied mutation, dispersal, and environmental period, and we believe



**Figure 5:** Influence of the three timescales (environmental fluctuations, evolution, and dispersal) on the structure of the metacommunity. The panels show different periods of the environmental fluctuations (A, period is three or 30 time steps; B, 300 time steps; C, 3,000 time steps; D, 30,000 time steps; E, 300,000 time steps). Simulations in which evolutionary branchings occurred are noted with a star.

that they capture all the possible qualitatively distinct behaviors of this simple system and adequately describe how they relate to these three parameters. The additional simulations presented in the appendix did not identify any additional qualitatively distinct outcomes and showed that the additional factors tested affected the outcome of the simulations in quantitative but not qualitative ways.

### Discussion

In spite of the increasing recognition that space (Loreau et al. 2003; Leibold et al. 2004) and evolution (Loeuille et al. 2002; Loeuille and Loreau 2004, 2005, 2006) play a central role in shaping the structure and functioning of natural communities and ecosystems, efforts to consider these two aspects together and the analysis of their interplay are still very few (Urban and Skelly 2006). The model we have presented here is built explicitly to address the fundamental question of the interplay of two simple component processes: the assembly process of species sorting that does not involve adaptive evolution and the evolutionary processes that determine whether adaptive evo-

lution within populations can occur. Our finding is that both processes interfere with each other and interact to produce an array of possible outcomes in metacommunities richer than predicted by either process alone.

We know of no current data that allow us to evaluate the predictions of these models directly, in either experimental or correlational studies. However, there is some evidence, though much of it indirect, that both of these processes (rapid local adaptation and species sorting) occur in natural communities. For example, zooplankton communities frequently respond strongly to various environmental factors (e.g., predation regime, water quality, lake morphometry) by undergoing changes in species composition (e.g., Tessier and Welser 1991; Cottenie et al. 2003). However, zooplankton also commonly show strong and rapid evolutionary responses to environmental change, often in response to these same factors (e.g., Tessier et al. 1992; Cousyn et al. 2001). What is not well documented is whether such adaptive responses influence the likelihood of eventual extinction by these zooplankton species in response to such change or whether they affect the likelihood of successful colonization by other species

and any consequent extinctions that may occur. Recent findings on genetically distinct populations of *Daphnia* suggest that differences in their abilities to prevent colonization by other species (Tagg et al. 2005; De Meester et al. 2007; J. H. Pantel and M. A. Leibold, unpublished manuscript) can regulate zooplankton community assembly.

There is similar evidence in many other systems that local adaptation and differentiation can be substantial (see Thompson 1997). For instance, the model presented may also give an adequate picture of systems such as sessile plants or marine fouling, for which patches may be described as aggregated microsites to be colonized. As with zooplankton, there is also evidence for strong patterns of association between local environmental conditions and species composition in these same systems. Our model indicates, however, that both outcomes can be important and that they may vary in a qualitatively predictive way with dispersal, mutation, and environmental periodicity. It also indicates that global monopolization may be present, but this is much harder to evaluate because it is hard to distinguish it from the possibility that there never was more than a single generalist species in a metacommunity. Suggestive evidence for such cases may come from studies on aggressively invasive species that show strong abilities to adapt to diverse local conditions.

Thus, evidence to either support or refute our hypothesis that local adaptation and species sorting interfere with each other in metacommunities as functions of dispersal, environmental change, and evolutionary potential is sparse and indirect. Nevertheless, the ideas are important in highlighting how these two fields of study may inform critical components of each other's dynamics. Our theoretical studies can thus serve as a conceptual starting point for conducting such studies.

Our goal in this article was to illustrate how species sorting and local adaptation might interfere with each other and that the outcome of having both processes occurring in a metacommunity might depend on the relative rates of dispersal, mutation, and environmental change. In this respect, our work clearly shows that this is so, but it is also likely that the interaction of these two processes is influenced by numerous other factors that we have not considered and leave to future work. Some of these are the following.

*Coevolution.* Here we have modeled the situation when only one component species is capable of evolutionary change. Evolution by the other species is likely to affect the outcome in important ways. We view the scenarios we have studied as an extreme in a continuum where the relative rates of mutation among component species might vary, but it is unclear what would happen when these rates become more similar. Convergence by all species, leading

to neutral local dynamics and coexistence in all patches, seems probable if all the evolutionary parameters (mutation and dispersal) are identical for all three species, but asymmetries in these parameters seem likely to lead to global monopolization or an intermediate in which there is also some species sorting.

*Evolution involving more than one trait.* We have modeled a very simple scenario where adaptation is related to only one trait, but traits involving local adaptation frequently are multivariate. Species may differ in how they respond to selection on a multivariate phenotype, and this seems likely to also affect the probable outcome in ways that are hard to predict.

*Evolution of food webs.* The tension between species sorting and local adaptation is perhaps most easily seen in models of competition such as the one we have used here. However, these processes are also likely important in evolutionary responses to traits that affect interactions with species in other trophic levels. Such interactions may behave in ways that differ strongly from the simple scenario for competition we have modeled. For example, adaptation to predators is likely to affect relative fitness among genotypes and species in how they are affected by a given density of predators (analogous to our model that involves simple tracking of density-independent environmental factors), but it will also affect how many predators will exist in communities and will thus alter relative fitness via this indirect pathway. It is unclear what might be expected from such indirect interactions.

*Evolution of plasticity.* In this model, we have assumed that all three species have a similar fitness function that differs only in the location of the mode. Plasticity would imply that these fitness functions could also differ in their other components (e.g., niche width  $\sigma$ ), with unknown effects on model results. As discussed above, if plasticity is sufficiently large, the model may converge on the neutral model with perhaps little consequence for either species sorting or monopolization.

*Evolution of dispersal rate and dormancy (seeds or resting stages of invertebrates).* Here we have focused on direct adaptation to local environmental conditions at the local scale and ignored adaptations that influence how species disperse or otherwise regulate the degree to which they are subject to selection by local environmental conditions. Dispersal and dormancy are two ways that organisms might otherwise adapt to such change. The effects, again, are likely to be complex. Note that evolution of dispersal and habitat specialization has already been shown as a possible mechanism of diversification and maintenance of diversity (Kisdi 2002).

*Landscape size and complexity.* Here we greatly simplified how we modeled the metacommunity to focus on three patches, and we simulated environmental change in one

patch in a very simplified way. It is likely that more complex situations will affect the results. Additional simulations presented in the appendix confirm that the five qualitative results we describe occur in more complex cases and that their qualitative relations to dispersal, mutation, and rate of environmental change are similar, though their boundaries in the dispersal/mutation space (fig. 5) are affected.

The model we presented gives two potentially important insights about the role of species sorting and monopolization in influencing the structure of metacommunities, in spite of its limits and complications. The first is that species sorting is a very likely outcome, despite local adaptation, whereas monopolization happens when dispersal is either very small (local monopolization) or high or when the evolution is very rapid (global monopolization). The dominance of species sorting may be related to the results reported in the meta-analysis by Cottenie (2005). Cottenie found that 44% of the metacommunities reported were most likely structured by species sorting and that an additional 29% were likely to be structured by a combination of species sorting and mass effects. This dominance of species-sorting processes has also been underlined by other metacommunity studies (Shurin 2000; Urban 2004). The other message of the model is that the two processes are not completely mutually exclusive and may be observed simultaneously even in the simple metacommunity we have introduced. Under these mixed intermediate conditions between species sorting and monopolization, we found that two species coexist in local communities, with identical or nearly identical adaptation to local conditions. This indicates that the interaction between evolution and community assembly can result in neutral dynamics (Bell 2001; Hubbell 2001) at the local scale, even if the interactions between these same species at the metacommunity scale is not neutral (Leibold and McPeck 2006). These intermediate cases are not rare in the simulations, and we expect them to be observed more often when refinements are added to the model. Such mixed outcomes also seem quite likely in more realistic and complex landscapes, where patches vary in their degree of isolation so that there are both isolated and closely connected patches simultaneously in the metacommunity.

The combined attention to evolutionary and metacommunity dynamics in these situations may thus be important in understanding patterns of species distributions across gradients in such landscapes. Furthermore, it seems likely that this interaction may also modulate numerous aspects of ecological responses to ecological change at large scales, including, for example, the responses to climate change or fragmentation.

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