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Author(s): Mathew A. Leibold and Jon Norberg

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## Biodiversity in metacommunities: Plankton as complex adaptive systems?

*Mathew A. Leibold*

Section of Integrative Biology, University of Texas at Austin, 1 University Station C0930, Austin, Texas 78712

*Jon Norberg*

Department of Systems Ecology, University of Stockholm, 10691 Stockholm, Sweden

### *Abstract*

One of the more intriguing and challenging developments in ecology and in limnology and oceanography is the expansion of the temporal and spatial scales that are being addressed by current work. Researchers are realizing that individual communities and ecosystems are not isolated from each other but rather that they are connected by exchanges of individuals (through dispersal) and materials (through spatial fluxes). From a conceptual perspective, there is a need to develop theories and hypotheses about the roles of these exchanges on different community and ecosystem attributes. Here we focus on the concept of metacommunities, to address how plankton communities are structured and how this may generate patterns of variation in planktonic ecosystems. Our premise is that planktonic systems can be understood in the framework of metacommunities and that the regulation of these metacommunities alter how they work as “complex adaptive systems.” We hypothesize that connectivity through dispersal of local communities that are embedded in aquatic metacommunities show a range of dynamic behaviors related to their capacity to respond adaptively to environmental change.

Much work in limnetic ecosystems has shown the rich array of community and ecosystem processes that regulate ponds, lakes, and larger bodies of water such as large lakes, seas, and oceans. This work has shown that limnetic ecosystems as a whole respond strongly to joint effects of abiotic resources (bottom-up effects) and of factors affecting organisms at the upper levels of the food web (top-down effects), in addition to other factors (e.g., Hall et al. 1970; Losos and Hetesa 1973; Leibold et al. 1997). These results correspond reasonably well to ecological models of community structure in food chains and in food webs (e.g., Phillips 1974; Oksanen et al. 1981; Leibold 1989, 1996). Arguably, limnetic ecosystems are among the best-documented cases that establish the links between local community dynamics and local ecosystem processes. To date however, most thinking about these effects has taken an approach that is strongly focused on local dynamics such as those that occur in the plankton of single lakes or ponds or in limited areas of larger water bodies (e.g., single basins or gyres in very large lakes and oceans).

Nevertheless, more recent ecological thinking (and some theory) is increasingly interested in how ecological dynamics are affected by processes that occur at a larger scale (e.g., Ricklefs and Schluter 1993; Tilman and Kareiva 1997; Holyoak et al. in press). It is tempting for limnologists, especially those who study smaller water bodies, to think that such larger scale processes do not necessarily influence lim-

netic ecosystems as much as they might other systems such as streams or terrestrial systems, where the movement of individuals and materials across local communities and ecosystem boundaries is more obvious. In the present article, we explore some of the ways that larger scale processes in limnetic ecosystems, which involve the dispersal of individuals relative to the connectivity among local systems, might influence how these ecosystems respond to local environmental change. We will argue that this perspective may strongly influence how well limnetic ecosystems act as “complex adaptive systems” (CAS; defined below), with emergent regular patterns in their attributes that result from these larger scale processes, despite variation in the identities of the component species that contribute to them.

We propose that linked sets of limnetic ecosystems (e.g., lake districts, wetlands consisting of many ponds, oceans, or very large lakes with multiple basins) can be interpreted in the framework of “metacommunities” (see also Cottenie et al. 2001, 2003). We then review what is known about theoretical metacommunities, focusing on the role of connectedness among local communities. We review evidence from planktonic systems about the degree of connectedness in different classes of limnetic ecosystems and argue that there is a continuum in this connectedness from lakes (least connected) to ponds in wetlands to local sites (e.g., gyres or embayments) in large lakes and marine systems (most connected) that should influence how we view the potential for these systems to conform to expectations of CAS. At this time, evidence about the degree of “adaptiveness” of these systems is insufficient for us to evaluate these ideas, so our discussion is highly speculative. Nevertheless, our goal is not to test these ideas but rather to provoke more consideration of these issues in limnetic ecosystems.

### What are metacommunities?

Metacommunities (Fig. 1) are sets of linked local communities connected by the dispersal of at least some of the

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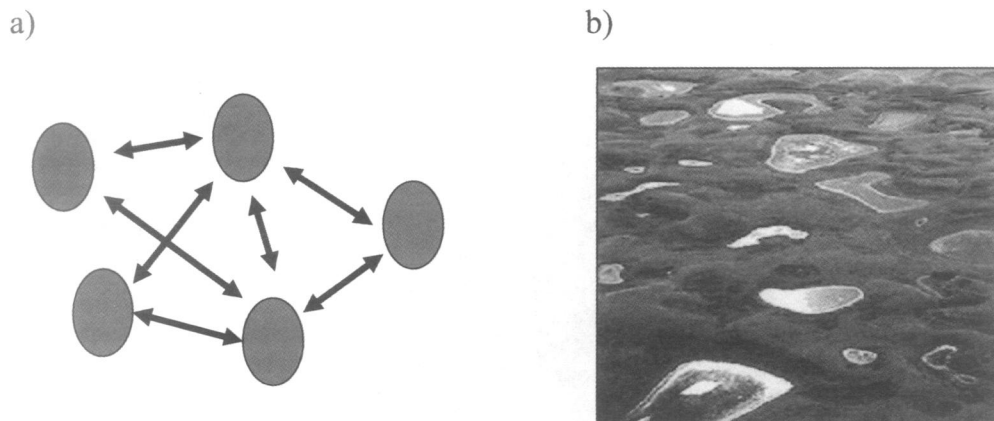


Fig. 1. (a) A diagrammatic representation of a metacommunity and (b) a visual example of pond metacommunities in prairie potholes. The metacommunity consists of multiple local communities (circles in panel a, ponds in panel b) connected by dispersal of individuals among ponds (arrows in panel a).

species involved (Gilpin and Hanski 1991). The idea is that the population regulation of abundances of species occurs at a local scale; in theory, this corresponds to the usual processes of density-dependent birth and death rates as they are affected by the ambient densities of resources and organisms. Conventionally, the effects of local environmental change would be modeled by local models of species interactions such as Lotka-Volterra equations of species interactions (and related approaches). Previous theory on the responses of local communities and ecosystems to such environmental change indicates that the responses should be highly unpredictable, because it is likely to be strongly context dependent (e.g., Levins 1975; Abrams 1993; Hastings 1996; Yodzis 1996). The lack of predictability to environmental change described in these simple models contrasts with the consistent/predictable responses to environmental change, despite the variations in food web and community composition that are often seen in unmanipulated systems (e.g., Cole et al. 1991; Leibold et al. 1997). There is evidence for this lack of generality in the responses of communities to local environmental change. For example, studies of plankton communities show that biomass responses of pond organisms to eutrophication vary with various aspects of food web architecture (e.g., Leibold 1989; Leibold and Wilbur 1992; Leibold et al. 1997; Hulot et al. 2000) in ways that do correspond to the context-dependent theory described above (*see especially* Abrams 1993).

At a larger scale however, metacommunities often involve many such local communities and some form of dispersal of individuals among them. We hypothesize that this dispersal can enhance the degree to which communities can respond predictably to environmental change to produce regular patterns between environmental gradients and community/ecosystem attributes. An example of such regularity is the predictable relationship between eutrophication and the biomass of plants and herbivores that contrasts strongly with the findings of local effects described above (*see* Leibold et al. 1997). This regularity can be explained by food-web models that involve such reorganization when open to dispersal (e.g., Oksanen et al. 1981; Leibold 1996). This happens because there is a compositional change in the communities in

response to eutrophication that leads to the emergent regularity in the joint responses of plant and herbivore biomass to eutrophication. This joint response is not predicted unless compositional change is involved. We argue below that thinking of community responses that incorporate compositional change can often explain such regularities if they are thought of as CAS, as discussed below.

We will focus on theories that assume no explicit spatial structure to the connections among local communities (although it is also possible, in principle, to develop a theory for models with such explicit structure). Thus, we assume, for simplicity, that dispersal rates are equivalent among all sites. This simplifies our discussion and allows us to make more general arguments than a spatially explicit approach (e.g., Durrett and Levin 1994; Pascual et al. 2001).

Dispersal has a number of consequences in metacommunities (Fig. 2), by either providing a source for colonizing

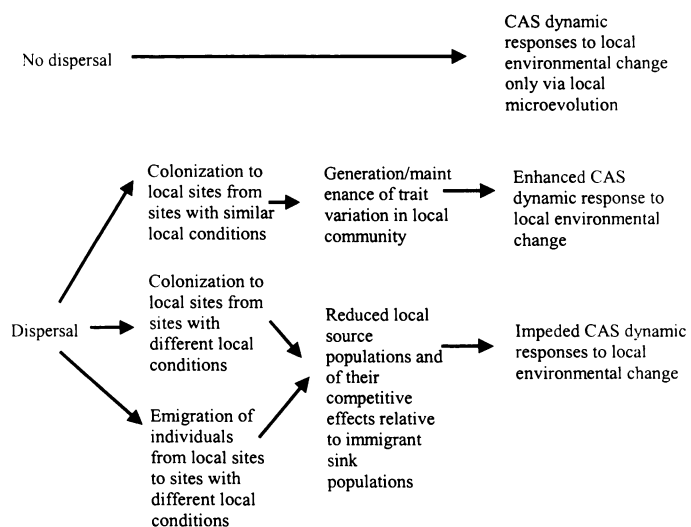


Fig. 2. Comparison of CAS dynamic responses to local environmental change in closed communities with metacommunities. Dispersal has three consequences that alter CAS dynamics in metacommunities. These three consequences may vary with connectivity, as described in the text.

species or by altering local population dynamics via emigration and immigration. The rate of migration depends on how high dispersal rates are in relation to the degree of connectance among sites (Leibold and Miller in press) and to the frequency of environmental change. If dispersal rates are low relative to the frequency of environmental change (e.g., disturbances, succession, or altered abiotic conditions), they are primarily important in regulating the “assembly history” of local sites (Post and Pimm 1983; Rummel and Roughgarden 1985; Drake 1990; Morton and Law 1997; Law and Leibold in press). That is, dispersal determines which species can be present at a local site, because it determines whether they have had the opportunity to colonize that site after appropriate (favorable) environmental change. If dispersal is very low relative to local population dynamics (the time it takes local abundances to reach some long-term stable behavior) and environmental change, local communities may be “undersaturated” in diversity or very susceptible to invasions because locally adapted “dominants” have not yet arrived at that site. When dispersal rates are high, this outcome becomes less likely to occur.

However, dispersal can play a second distinct role when it is high enough that local population abundances are significantly affected by both the emigration of individuals and by the immigration of individuals from other sites via “source-sink” relations among sites. Dispersal under these conditions can also alter communities by supporting populations at local sites that are not self-sustaining, by having such populations competitively suppress other populations that would be self-sustaining and potentially driving them extinct, and by leading to sufficiently high losses in the source populations (due to emigration) that they are, in turn, suppressed or driven to extinction (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002).

Both altered assembly histories, which are contingent on the distribution of species at other sites and source-sink relations among sites, can in theory alter local dynamics of communities (*see* Leibold and Miller in press for a review); as a consequence, communities possibly alter ecosystem features of the system.

In some cases, the analogy between metacommunities and limnetic systems is striking and obvious (*see Fig. 1*). In small water bodies (ponds and smaller lakes), for example, the mixing and local movements of planktonic organisms is generally thought to be high enough that the entire lake or pond can be considered a local site with reasonably well-mixed individuals. Dispersal between these water bodies is low (Caceres and Soluk 2002; Havel et al. 2002; Cohen and Shurin 2003; Havel and Shurin 2004), so that it is unlikely to result in source-sink relations (Cottenie et al. 2003). Nevertheless, the species pool available to alter local communities may still come from a fairly large area in the landscape of local sites (Shurin et al. 2000). In other cases, the analogy may appear to be a bit less obvious. In large lakes and marine systems, for example, the regulation of population densities probably occurs on scales that are smaller than the entire water body, perhaps being limited to individual gyres, basins, or other, smaller, spatial scales (e.g., Patalas and Salki 1992, 1993). However, these subcomponents of water bodies are connected by the dispersal of organisms, and much of

this dispersal probably occurs passively via the movement of water in potentially complex ways. The amount of mixing of individuals that occurs within and among these subareas of the water bodies is probably much less distinct, and it is possible that many local populations of organisms have dynamics that strongly reflect the rates of emigration and immigration to and from other areas of the water body (e.g., Miller et al. 1998). Thus, in different types of limnetic systems, there may be a continuum of possible metacommunity dynamics, depending on how strongly interconnected local communities are by dispersal.

### What are CAS?

Ever since Forbes (1887), limnologists and aquatic ecologists have been interested in the organization of limnetic ecosystems and have identified certain properties of these communities and ecosystems that seem to emerge from the combined effects of abiotic and biotic processes. These properties include trophic structure, the partitioning of biomass among functional groups (e.g., Leibold 1989; Hairston and Hairston 1993; Leibold et al. 1997), characteristic bounds on nutrient stoichiometry (Sterner and Elser 2002) and nutrient availability (Leibold 1997), and regular patterns of species distributions and diversity relative to environmental gradients or seasonal changes in eutrophication, mixed layer-depth, and pH, among others (e.g., Reynolds 1984; Tessier and Horwitz 1990; Leibold 1999; Tessier and Woodruff 2002).

These regular patterns of organization involving community properties are a challenge to our ecological theories. Community ecology theory based on complex food webs and webs of interacting species predicts that responses of communities to local environmental change (either abiotic or biotic) should be very idiosyncratic and depend in complicated and context-dependent ways on the composition of the community (e.g., Abrams 1993; Hastings 1996; Yodzis 1996). The conclusion is that almost any pattern between environmental change and attributes of the community or ecosystem might be expected without detailed knowledge of the dynamic relations among all of the organisms in the community (Schaffer 1981). Indeed, locally restricted experimental manipulations of nutrients, for example, show just this sort of context dependence in affecting trophic structure (Leibold and Wilbur 1992; Leibold et al. 1997). How do regular patterns of ecosystem properties emerge despite such context dependence? Can such regular patterns be explained by processes involving metacommunity dynamics? Early suggestions that ecosystems could ‘evolve’ adaptively to explain these features of ecosystems by a process akin to Darwin’s theory of natural selection were strongly discounted by skepticism about the level of group selection needed (but *see* Wilson 1992 for modified arguments about group level selection in metacommunities).

We focus on the idea that communities at various scales consist of multiple interacting components that can reorganize their relationships depending on the environmental context. One approach to understanding how this occurs uses the theory of CAS (Holland 1996). It provides a basic un-

Understanding for how patterns and dynamics of aggregate community variables such as total biomass and productivity, as well as different measures of diversity and trait distributions within the community arise (e.g., Levin 1998, 1999; Levin et al. 2001; Norberg et al. 2001; Norberg 2004). In a recent review, Levin (1998, 1999) identified the following three criteria as the basic ingredients of CAS:

1. Sustained diversity and individuality of components. Here we argue that dispersal among heterogeneous sites within a metacommunity can help maintain this diversity.
2. Localized interactions among those components. In metacommunities, dispersal can compromise the local interactions because immigration and emigration disrupt the localized nature of the interactions in relation to local context. If dispersal among local communities is so high that individuals interact with individuals at other sites just as much as they do with individuals within sites (e.g., over their lifetime), then this “well-mixed” system does not have localized interactions and does not qualify as a CAS.
3. An autonomous process that selects from among those components on the basis of the results of local interactions. Overall, the effectiveness of this process will be altered by the conflicting effects of dispersal described above in (1) and (2).

Thus, CAS describe a concert of three main processes that can occur in metacommunities, one creating and maintaining diversity in local communities, one of interactions between these species, and one that selects the resulting diversity in form and function in response to local environmental context. The net result is that the assemblage of species continuously changes toward a dominance of those best suited to deal with the selective forces of the environment. As a consequence, the traits of the system components (functional groups of species in the case of ecosystems) vary in a predictable way relative to local environmental conditions.

For example, we may be interested in how local changes in N and P loading rates may alter which algae come to dominate a local ecosystem and how this determines the relative availabilities of N and P. In a simple model of resource competition (Fig. 3), the ecological traits of interest are the minimum requirements for N and P of the various species in the community and the associated tradeoffs in specific growth rates. The environmental variables of the system are the local total concentrations of N and P determined by extrinsic loadings and internal uptake rates. One emergent macroscopic property of the system subject to optimization is the resulting level of the resource depletion capacity of the community for N and P (the resulting availabilities of the two nutrients).

We define the ability of a community to change its properties in response to changing local environmental conditions (or constraints) as the “adaptive capacity” of the system. The adaptive capacity of an ecosystem in ecological time (not evolutionary time) is caused by a change in its components (species) by species sorting processes (succession driven by community interactions—resource competition in this case) and the ability to sustain a diversity of components with different traits. In support of this view, we find that trait

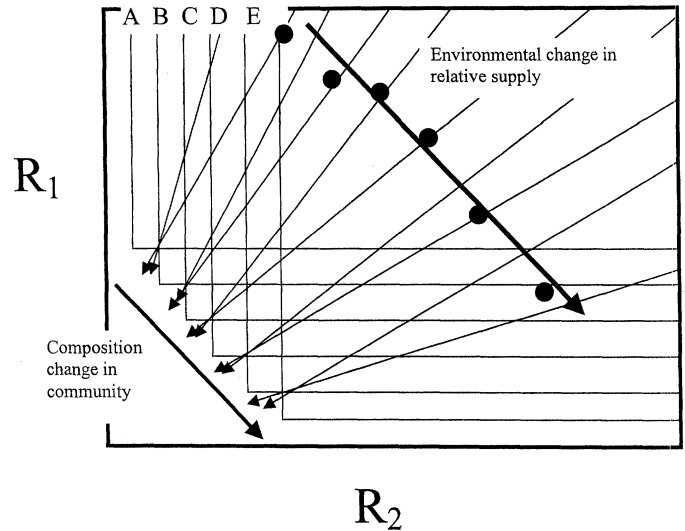


Fig. 3. Effects of variation in relative supply of two nutrients on the outcome of competition in a guild of competing plant consumers (modified from Tilman 1982; see Leibold 1997). Environmental change in the relative supply of the two nutrients (illustrated by the upper arrow and solid points) is associated with a change in the composition of species with different minimum resource requirement traits. This is illustrated by the lower arrow that is near the sequence of equilibrium points (intersection of the thin lines depicting each of their zero net growth isoclines) associated with this change. This change in the local environmental supply of the two nutrients leads to a regular predicted parallel change in nutrient availabilities that is dependent on the process of compositional change, determined by the selective process of resource competition. However, because only two species are predicted to coexist in any steady environment, the process can only occur if there is a source of colonization for species that are absent.

variance, as well as genetic variance, is proportional to the rate of succession of the average trait in the community (Norberg et al. 2001) in a way that is very similar to models of the rate of evolution according to Fisher’s (1958) fundamental theorem of natural selection.

In the context of ecological processes, any community that exhibits the ingredients of CAS—for example, sustained diversity by immigration from a regional species pool or resting stages, local interactions such as competition for resources and predator-prey interactions, and a selective process among these components—will show continuous succession and an ability to change its composition in response to changes in the selective processes. Below we will refer to this selective process as “species sorting” and use metacommunity thinking to evaluate how effectively the species sorting process might work under different levels of connectivity to ask how much species sorting might contribute to regularity in the emergent patterns of ecosystem attributes we mentioned above.

The obvious links between these features of CAS and many models and descriptions of local communities and ecosystems make it tempting to apply ideas of CAS to understand how communities and ecosystem attributes (such as trophic structure or patterns of biodiversity) are regulated. In the present article, we will focus on evaluating how the

composition of communities and the consequent cumulative roles of species in these communities respond to simple directional changes in the environment. We focus on situations in which species sorting leads to regularity of patterns that are not found in models that do not allow for adaptive compositional change (it is also possible for CAS to produce irregular patterns or sensitivity to initial conditions; *see* Levin 1998).

For example, the eutrophication of waters by nutrient inputs of phosphorus and nitrogen has well-documented and consistent effects on trophic structure and nutrient availabilities that contrast with the results of locally constrained experiments mentioned above (*see* Leibold et al. 1997). How important is the species sorting process in regulating these effects and others like them? Our premise is that species sorting will be more effective in some metacommunities than in others, depending on how closely connected local sites are and how this affects the three processes that make an ecosystem a CAS.

### How does dispersal affect the adaptive capacity of ecosystems?

We focus on the connectedness of local sites via dispersal and argue that the degree to which emergent regularities will occur in limnetic ecosystems will be maximal at intermediate levels of connectedness (*see* Fig. 2). If connectedness is too low, so that local communities are undersaturated or open to invasion because of dispersal limitation of locally adapted dominants after environmental change, then the degree to which these emergent properties will occur will be lessened. Alternatively, if connectedness is so high that emigration can substantially reduce the local effects of dominants on ecosystem attributes or if immigration from other sites by species that are not locally adapted alters local ecosystem processes (Mouquet et al. 2002; Loreau et al. 2003), then the degree to which these emergent regularities occur will also be lessened.

We use the theoretical framework of Norberg et al. 2001 (*see also* Norberg 2004) to relate macroscopic community and ecosystem properties to the internal dynamics of the system via a selective process that matches the ecological traits of species and the extrinsically determined properties of the system. The following theory makes our verbal arguments more explicit and links them to other work done on CAS. Specifically, we want to relate community dynamics to different levels of dispersal from a broader metacommunity, to ask how well the traits of species in local communities correspond to those that are expected to optimize some macroscopic property of the system that varies along some environmental gradient. For simplicity, and as in Norberg et al. (2001), we will look only at one variable factor involved for such a gradient, that we index using  $E$  (*see* Norberg 2004 for applying the framework to multiple and interacting factors). In the example we described above, this could be the ratio of N:P loading rates: for example,  $(S_N/S_P)$  in Fig. 3). We then define a function that which relates the specific growth of an individual species with trait  $Z$  to the environmental constraint,  $E$ , as  $f(E, Z)$ . In our example, the

trait  $Z$  would correspond to different relative minimum resource requirements for N and P (i.e.,  $N_i^*/P_i^*$  in Fig. 3). This function has the property that, for any numerical value of  $E$  (i.e.,  $S_N/S_P$ ), there exists only one trait,  $Z_{opt}$ , with optimal growth such that species with this trait are the competitive dominants. Thus, one might think of  $Z_{opt}$  as being a direct function of the environmental variable such that the optimal trait is given as  $Z_{opt}(E)$ . The community properties then are the distribution of traits,  $C(Z)$ , i.e., biomass of species with trait,  $Z$ , and total biomass,  $CT = \int c(Z)$ . When the environment,  $E$ , is constant over time, the distribution of traits will asymptotically go toward zero variance (competitive exclusion), with a mean close to  $Z_{opt}$  depending on whether a species with such a trait is present in the system. In real systems, this may be constrained by how variation is partitioned within and between species, and, if there is not sufficient intraspecific variation, there may still be multiple species present, but they will tend to converge in their traits (*see* Leibold 1998). This convergence may maintain high taxonomic diversity despite low trait diversity, especially if it leads to equivalent species that replace each other via demographic stochasticity and can be influenced by other slow evolutionary processes such as speciation (*see* Hubbell 2001).

We can then build on this framework to see how dispersal affects the CAS dynamics. There are several mechanisms for how the trait distribution in the local ecologically active community (i.e., excluding inactive resting stages) may be kept from zero trait variance, including the mutation of component species and phenotypic plasticity, but we focus on immigration and emigration of species with fixed traits. In this case, traits that are only present in very low abundances will eventually go extinct; thus, the active trait distribution will tend to lose its tail ends. The replacement of these tail ends then can only occur by dispersal from a regional source pool or from resting stages (dispersal through time) from which new populations can establish. Thus, we may distinguish the local active trait distribution,  $C(Z)$ , from the trait distribution of arrivals by dispersal  $D(Z)$  or hatching from resting stages  $R(Z)$ . Total community dynamics in one patch,  $i$ , is then described by

$$\frac{dC_i(Z)}{dt} = f(E, Z) \times C_i(Z) + D_i(Z) + R_i(Z)$$

if we assume that emigration rates are density dependent and incorporated in  $f(E, Z)$ .

Because the units are in biomass (or abundances), we expect that sometimes the total input from dispersal  $\int D_i(Z)$  and resting stages  $\int R_i(Z)$  will be very small compared with total community biomass,  $CT$ , and hence contribute little to total productivity (but this may not always be the case; *see* below). However, this input may be crucial for the adaptive capacity (as defined above) of the community, because we can expect the variance especially of  $D(Z)$  to be greater than both  $C(Z)$  and even of  $R(Z)$  if the range of temporal changes in  $E$  is smaller than the spatial range of  $E$ . In the following, we will focus on the dispersed trait distributions.

For any pond or lake,  $i$ , the trait distribution of arrivals by dispersal,  $D(Z)$ , is given as

$$D_i(Z) = \sum_{j \neq i} d(Z) \times C_j(Z) \times k(s_{ij}, Z)$$

where  $d(Z)$  is the fraction of biomass,  $C_j(Z)$  with trait  $Z$  which disperses from each other site (not equal to  $j$ ),  $s_{ij}$  is the distance between patch  $i$  and  $j$ , and  $k(s)$  is a dispersal function (kernel) that relates distance, trait value, and the number of individuals arriving at site  $i$ . Note that both  $d(Z)$  and  $k(s, Z)$  can depend on the trait—for example, if energy allocation tradeoffs for dispersal interact with the trait for which we assume that local species sorting processes are important. One might, for example, envision that species with good resource-harvesting mechanisms have less energy available for producing efficient dispersal propagules. This may cause a shift between in the mean of  $D_i(Z)$  and the actual mean trait in the regional pool of traits. This discrepancy may influence local properties and prevent the community from reaching trait distributions in which the mean is close to  $Z_{\text{opt}}$ .

In our discussion, we have assumed that the variance in the trait distribution of the regional biota is greater than the distribution in local communities. At some level, this is likely to be true, because the local community is a subset of the larger regional biota. However, the degree to which this is true will vary. If the metacommunity is very highly mixed, for example, the system collapses to having the same trait distribution at both scales. Exactly how the regional trait distribution is regulated is an interesting question in its own right but is relatively understudied (Amarasekare and Nisbet 2001; Mouquet and Loreau 2003).

Let us now envision three different scenarios with respect to the importance of  $D(Z)$  relative to  $C(Z)$ . All scenarios assume that the variance of  $D(Z)$  is larger than the variance in local environmental fluctuations such that potentially there is always one  $Z_{\text{opt}}$  for any possible value of  $E$ . To make the scenarios more interesting, we will also assume that, because of tradeoffs, the mean of  $D(Z)$  is different from the mean of the local optimal trait.

*Underdispersal*—In this scenario, we assume that the arrival of individuals is very low, such that colonization events are very stochastic in an ecological timescale. Because the mean of  $D(Z)$  is different from the mean optimal trait, we would expect that species with suboptimal traits have a greater chance to establish themselves. Using the above example, this could result in a community with low resource-harvesting efficiency. Furthermore, if the local environment is very different from the regional average environment, the chances of species with locally optimal traits establishing themselves may be very limited. The general effect of underdispersed communities would be a larger probability of having a local trait distribution with a mean, which differs from the average locally optimal trait as well as reduced trait variance because of limited recolonization events. The former reduces ecosystem functioning, whereas the latter reduces the adaptive capacity of the community.

*Overdispersal*—In this scenario, we assume that the amount of arrivals by dispersal is high relative to the local abundance—that is, that  $[\sum D_i(Z)]/[\sum C_i(Z)] \gg 0$ . This means that the actual biomass coming into the community by dis-

persal is substantial and affects both ecosystem processes but even more the local trait distributions. In effect, this means that local species-sorting processes are overruled by the immigration process such that the local average trait is biased toward the average trait of the immigrating community even if the strength of the local sorting processes is very high. As in the previous scenario, we expect to find a community with a suboptimal trait average, but, in contrast, to the previous scenario, one might expect a larger trait variance. Note also that high trait variance per se decreases community productivity relative to that of a community that has a trait distribution at the optimum because of a larger fraction of the biomass having suboptimal traits.

*Medium dispersal*—In this scenario, colonization is not limited by dispersal rate of species with given traits—that is, colonization occurs often enough to maintain an active population of any species that can grow at a single point in time along the whole trait distribution. However, dispersal is also not so high that it affects community properties by supporting suboptimal species due to immigration or by decreasing the density and effectiveness of locally optimal species by emigration. Most important, the community always has a stock of suboptimal species (passenger species sensu Walker et al. 1999) that could potentially become dominant if favorable conditions occur (i.e., a high adaptive capacity).

What roles do dispersal and differential ecological performance play in plankton systems?

The key point is that species sorting contributes most strongly to producing the regular patterns between aggregate features of ecosystems and local environmental conditions expected from CAS when connectedness is intermediate. This corresponds to situations in which dispersal is intermediate relative to the frequency of environmental change. A comprehensive review of dispersal in plankton is beyond the scope of the present article (see Havel and Shurin 2004), but we can focus on some major features, especially if we focus on zooplankton. There are two major issues: (1) identifying situations in which local communities have species compositions that are dispersal limited versus those that are not (i.e., separate situations in which species sorting is limited by having constrained assembly histories from those that do not) and (2) identifying situations in which species sorting is constrained by too much dispersal, so that emigration of locally optimized species or immigration by species optimized to different conditions prevents species sorting from playing an important role in the regulation of local emergent ecosystem attributes.

An important complication in plankton systems is the importance of resting stages. Such resting stages represent individuals that are not ecologically active and thus are protected from environmental change as well as from having little effect on the active part of the population. They can be thought of as “dispersal in time,” in contrast with the normal view of dispersal in space that we emphasized above. Many of their consequences will be very similar, however. One important way in which they might differ is that they en-

hance adaptiveness when it involves environmental change that has already occurred and is less likely to be important in situations that involve novel environmental change.

We focus on very coarse distinctions among ponds, deep (generally stratified) lakes, and large water bodies (seas, oceans, and very large lakes). As was mentioned in our introduction, we view metacommunities of ponds and lakes as being composed of local ponds and lakes that are separated by terrestrial habitat from other such water bodies. However, we refer to large water bodies for systems that are so large that they do not function as single homogenous communities but rather can be viewed as a metacommunity of smaller units such as gyres or embayments, in which mass transport from one unit to another is important. Often, the three systems (ponds vs. deep lakes vs. large water bodies) have quite distinct biotas (at least with regard to zooplankton), so that we can evaluate them independently from each other. We recognize, of course, that there will be situations in which particular examples of each of these will not correspond to the general conclusions we make, and we hope that reasons for this will be obvious. For example, lakes connected by streams may have higher dispersal rates than isolated ponds, even though they are farther apart. Also, our discussion of these issues is highly speculative, with the goal of stimulating thought on these topics. We also recognize that the evidence we will provide is scant and may even be contradictory, but we hope that it provides an intriguing organizing framework for comparative studies of plankton systems.

*Pond metacommunities*—Ponds often occur in landscapes where they tend to be less distantly separated than are deeper lakes (Fig. 1). For example, the average nearest distance between ponds in southwestern Michigan (Shurin 2000, 2001; Shurin et al. 2000) is  $\sim 60$  m, whereas the average nearest distance among deeper lakes is on the order of  $\sim 1$  km (Shurin pers. comm.). Of course, there are exceptions in which ponds are much more isolated, and we might hypothesize that their dynamics would be correspondingly different.

In a set of manipulative in situ experiments in a landscape of ponds in southwestern Michigan, Shurin (2000) found that local zooplankton communities are surprisingly resistant to invasions by species in the larger species pool that characterizes the entire region or metacommunity. He also found that there was a negative relationship between the probability of invasion by absent species and the local diversity of the ponds. Finally, he also found that those species that did invade never became very common and that these invasions were not associated with any documentable effects on other species in the community. This final result suggests that the species that were absent from the local community, but that could invade, would be among those most likely to subsequently go extinct. One conclusion might be that local communities in these ponds consist of the species that are the dominants and that no such dominants have distributions that are limited by dispersal in these metacommunities of ponds. These ponds undergo fairly substantial rates of environmental change (drying, nutrient pulses from rain events, and altered predation regimes associated with predator dynamics; Skelly et al. 1999; M.A.L. unpubl. data) that are associated with compositional change. Apparently, dispersal is never-

theless high enough that there is very little dispersal limitation of composition. Although there is some dispersal limitation present in these metacommunities, it seems to involve species that are locally peripheral (at least for the ponds in which they are absent). Overall, this suggests that dispersal is high enough to allow species sorting to occur in these systems.

In contrast with these studies, Jenkins and Buikema (1998) studied the role of dispersal in structuring zooplankton communities of newly formed ponds in Kansas. They found that ponds with very similar local abiotic conditions developed different zooplankton communities over the first year of existence of the pond, depending on dispersal limitations. That study, however, focused on this initial period of pond assembly, and it is unclear how the longer-term metacommunity behavior of ponds would be affected. Steiner and Leibold (in press) found, in theoretical models of food web assembly, that there can be a substantial period of dispersal limitation during the early parts of the assembly process but that this disappears later as the assembly process continues.

Dispersal could also be so high that local adaptability is compromised by influxes of dispersal from nearby ponds, and this could prevent species sorting from effectively tracking local environmental change. An elegant study by Cottenie et al. (2001, 2003) studied this problem in a metacommunity of ponds in Belgium. In contrast with the ponds studied by Shurin et al. (2000), the Belgian ponds were strongly interconnected by water flow between them via short streams and canals. Thus, dispersal among ponds was probably substantially higher in this system than in the system in Michigan and most other common sets of ponds. Cottenie et al. (2001) measured dispersal rates between adjacent ponds using drift nets in the connecting streams and evaluated how such dispersal might have influenced the composition of adjacent ponds with very different local environmental conditions related to top-down effects of fish predators. They were able to show that such dispersal could sometimes be shown to affect the composition of downstream ponds but that this only occurred on rare occasions when flow rates were very high ( $>1\%$   $d^{-1}$  by volume). More commonly, local species interactions appeared to be strong enough to prevent strong effects of dispersal, despite the unusually high (for ponds) rates of immigration. Cottenie et al. (2001) thus showed that the dispersal of zooplankton is generally too low to strongly affect the process of species sorting in pond metacommunities, even in situations in which dispersal is unusually high for such systems.

We thus speculatively hypothesize that dispersal in typical pond metacommunities generally does not limit assembly dynamics, nor does it swamp local interactions to prevent species sorting from occurring. These are the conditions in which metacommunities most strongly act to work like CAS. We might therefore expect pond systems to be highly resilient in their responses to environmental change.

Is there any evidence that pond ecosystems can have resilient system attributes? Leibold and Smith (in press) studied the effects of enhanced nutrient levels in a set of experiments conducted in artificial pond systems. They examined how eutrophication by nutrient inputs altered trophic struc-

ture in pond-mesocosm communities that had faunas derived from inoculae from representative oligotrophic and eutrophic ponds. They contrasted this with the effects in pond communities that received mixed inocula from both types of ponds. They found that trophic structure and relationships between herbivore and plant biomass were log-linear only in the case with mixing from both oligotrophic and eutrophic ponds but that there was no consistent relationship between herbivore and plant biomass in either cases when biotas from single ponds or mixed biotas from ponds that had similar nutrient levels were involved. These cases with more restricted species sorting instead showed unpredictable responses, with algal biomass sometimes showing very strong responses in the absence of significant herbivore responses or vice versa. The relationship between herbivore and plant biomass in the mixed dispersal situation corresponded to previously documented relationships in natural ponds, whereas the relationship in the more restricted situations did not and instead resembled the results previously obtained in experiments conducted at the local scale (Leibold et al. 1997). Thus, dynamics of pond systems with enhanced species sorting showed regularities in the dynamics of aggregate properties that were absent in closed systems, which suggests a strong role for CAS regulation. Because the pattern observed in the treatments with high dispersal corresponded closely to observed biomass relationships in natural ponds (see Leibold et al. 1997), this implies that such natural systems also act as CAS.

*Lake metacommunities*—We can compare these results from pond systems with studies conducted in larger lakes. These systems have fairly distinct zooplankton species, with many dominant species that are absent from ponds even when they co-occur in a common landscape. One of the main reasons is probably the presence of stratification, which can provide refuges from strong predators and alters the dynamics of resources. Many of the dominant species show behaviors that exploit the resulting vertical habitat gradients, and this appears to be important in regulating species interactions in these systems in a way that does not occur in ponds (Leibold and Tessier 1997).

It is reasonable to think that such lake metacommunities are substantially less interconnected than ponds because they are generally less tightly distributed in the landscape, even though the mechanisms for dispersal are generally similar (see Havel and Shurin 2004). For example, Havel et al. (2002) have evaluated the dispersal kernel of an invasive *Daphnia* species and found that it only dissipates at a distance of ~20 km. This distance is often comparable to the interlake distance but greatly exceeds that for many pond wetlands. The frequency of environmental change is also likely to be less in these lakes than in ponds, largely because their hydrologies are much more stable (no drying up) and because nutrient pulses are perhaps smaller relative to the mass of the water body (lower perimeter/volume) unless the lakes are fed by streams from large watersheds. Nevertheless, dispersal limitation may still constrain how these communities respond to environmental change when it occurs.

There are a number of documented cases for the dispersal limitation of zooplankton communities in these situations.

For example, McNaught et al. (2004) documented the effects of accidental introductions of *Leptodora kindtii* in a small stratified lake in Michigan. Previous work had shown that this species had long been absent (perhaps never present) from this lake. McNaught et al. (2004) showed that this introduction led to a large population boom for *Leptodora*, a result that contrasted with the outcome of any of the introductions documented by Shurin (2000) in his ponds. They also showed that this introduction strongly altered the remaining community, also in contrast with the findings of Shurin (2000, 2002) in ponds.

Knapp et al. (2001; see also Sarnelle and Knapp 2004) also examined dispersal limitation in California Sierra alpine lakes. The artificial stocking of trout in these lakes has led to a documentable loss of species including the dominant grazers *Daphnia middendorffiana* and *Hesperodiaptomus shoshone*. They examined how long it took for *Daphnia* to recolonize and regain its dominant status in these lakes after the experimental extirpation of stocked trout populations. They found that this took 1–4 yr. *Hesperodiaptomus*, in contrast, seemed to be unable to recolonize, even though there was a viable egg bank, perhaps because of Allee effects that limited mate finding. Lakes may be more subject to such Allee effects than much smaller ponds in which mating may not be as strongly limited at small population sizes. A similar study of recovery of *Hesperodiaptomus arcticus* in another alpine lake also showed that it was strongly dispersal limited (McNaught et al. 1999) and did not recover from extirpation of fishes until it was reintroduced. McNaught et al. (1999) showed that the increase by *Hesperodiaptomus* was associated with strong shifts in other zooplankton populations (especially rotifers) and in the size and taxonomic composition of phytoplankton. Similarly, after the accidental introduction of *Diaptomus pygmaeus* into a small lake (probably during an experiment by N. Hairston Jr., pers. comm.), the native water-column population of *Diaptomus sanguineus* became virtually extinct (except for hatching from the egg bank, in which eggs survive for many decades; Hairston et al. 1995). Since the introduction, *D. pygmaeus* has become dominant in the plankton, which indicates that, in the past, it may have been dispersal limited despite being competitively superior to *D. sanguineus*.

These various examples together indicate two things. First, they indicate that the local community composition of zooplankton in lakes is more strongly dispersal limited than was found in ponds. Often, it took several years or it took artificial inoculation before expected dominants were reestablished in these lakes after environmental change. Second, they indicate that many of the species that did become dominant after such changes were important in affecting the local communities, including the size and taxonomic distribution of phytoplankton.

Nevertheless, there are also studies that have shown some tracking of environmental change in lakes (e.g., Mittelbach et al. 1995), although sometimes with some apparent lag (e.g., Edmondson and Litt 1982). The dynamics in such situations may well be related to effects of resting stages (“dispersal in time”) but are constrained by the viability of the resting eggs (Hairston 1996; Caceres 1998; Caceres and Tessier 2003) and can only occur in relation to recurrent envi-

ronmental change rather than changes associated with novel local conditions. Lakes that are connected to appropriately inhabited species via streams may also respond faster than those that are not. Nevertheless, historical studies are hard to interpret unless they are associated with known colonization events or have very tight sampling schedules, because lags may be caused by dispersal limitation or to more subtle effects of temporal change.

Another way to look at dispersal limitation is to focus on spatial autocorrelations in community structure. In well-optimized CAS with close correspondence between local composition and the optimization of aggregate community properties, most of the spatial variance in local community structure should be explained by local variance in extrinsic "driving" variables. When this is not so and there is substantial "unexplainable" spatial variance or local autocorrelation (explainable only by purely spatial effects of proximity among sites), this indicates that systems that do not have as close a match between local environmental conditions and local community composition. This could either be due to dispersal limitation, where nearby lakes have similar compositions because optimally adapted species have not been able to colonize appropriate local lakes, or to overly dispersed systems, where dispersal from nearby sites swamps the local effects of species sorting. Sophisticated statistical analyses of zooplankton communities in lakes have indicated that there are purely spatial effects that cannot be explained by known environmental variables (Pinel-Alloul et al. 1995). This is presumably caused by effects of dispersal in limiting the distribution of species from all the sites where they would be predicted to occur on the basis of local environmental conditions. Cottenie et al. (2003) conducted similar analysis on pond metacommunities and generally found no spatial effects, except when they were able to document the effects of immigrations on local population dynamics. However, these were more likely due to source-sink effects between closely linked ponds rather than dispersal limitation (such source-sink relations are not likely in the lakes studied by Pinel-Alloul et al. 1995).

Finally, some studies of lakes have shown that there can be substantial amounts of compositional turnover of species from one year to the next (Arnott et al. 1999; Leibold et al. unpubl. data) that does not seem to be related to environmental change in any obvious way. These may indicate dispersal limitation in these lakes, although they may also indicate that there are complex patterns of community assembly in such communities (*see* Steiner and Leibold in press for theoretical models that predict such patterns).

Taken together, these various lines of evidence suggest a stronger limitation of assembly dynamics by dispersal in lakes than in ponds, and we hypothesize that this will result in a weaker contribution to the processes of CAS. Thus, lakes may respond more slowly to environmental change and may be more strongly disrupted by such change than ponds.

Nevertheless, lakes also show fairly strong evidence of being organized according to the predictions from CAS. For example, like ponds, they show strong log-linear joint relationships of plant and herbivore biomass with eutrophication in unmanipulated lakes and in lakes that have been eutrophicated for relatively many years. However, short-term ad-

ditions of nutrients in whole-lake studies have not shown corresponding patterns, nor have they shown compositional change (perhaps because of dispersal limitation) in experiments that have lasted <3 yr (Leibold et al. 1997).

*Large water-body metacommunities (very large lakes, seas, and oceans)*—In very large water bodies, the strong distinction between local and regional (metacommunity) dynamics becomes weakened, because they are not so clearly demarcated by terrestrial habitat. In these systems, different parts of the water body have dynamics that can be distinct, and the population regulation via non-spatially regulated dynamics (corresponding to our usual notions of local species interactions) occurs on a much smaller scale than the entire water body. Patalas and Salki (1992, 1993) provided evidence for such patterns and the influence of dispersal in generating them for large freshwater lakes, as well as showing that patterns are much weaker in smaller lakes. The actual dynamics of very large systems can be greatly complicated by space itself in such cases (e.g., Pascual et al. 2001), but we can use simpler metacommunity theory and consider what happens when dispersal is high enough to constrain species sorting via source-sink relationships among different sites (Amarasekare and Nisbet 2001). The important issue here is when these sites (localities within the water body) are different in some environmental factor such as nutrient level, predator control, or another similar factor. Work done in metacommunity theory has indicated that the local optimization of ecosystem attributes (such as productivity in competitive communities) will be constrained if such migration among heterogeneous sites is too high (Amarasekare and Nisbet 2001; Mouquet et al. 2002), and these indications are consistent with our simple models of CAS under high dispersal described above.

We hypothesize that this may most likely be the case in large water bodies, because these are the limnetic systems in which such dispersal is most likely to be high enough relative to local species interactions to disrupt species sorting in response to local environmental differences. Spatiotemporal demographic analyses of individual zooplankton species in such systems have often indicated the presence of large populations that have no apparent long-term sustainability in these systems. For example, detailed studies of *Calanus finmarchicus* in the North Atlantic using individual based models reveals that there are only a few areas or basins that have self-sustaining populations (Miller et al. 1998). In addition, high densities of individuals in other areas can be supported by advection in areas where they cannot subsequently recruit. If these high densities play important roles that affect other species in these areas, including competitors, resources, or consumers, then they could modify these local communities in important ways. Two points are important in these cases: first, the movement of individuals via advection to areas where they are assured to be unsuccessful in reproducing is the equivalent of mortality for the source populations they come from. This should strongly compromise their abilities to reduce local resources or serve to sustain local consumers even in these "source" areas. Second, and in contrast with mortality, these individuals continue to alter resources and serve as food for con-

sumers in potentially strong ways at other “sink” locations where they may reach high densities. If the source area for the population were closed to emigration, this species would thus have a much greater survival rate, and simple ecological theory would predict that it would have a much stronger local role in regulating its resources and its consumers in this area. Additionally, it would have weaker (and potentially no) effects in areas where it currently exists as a sink population, potentially facilitating other species.

One of the more important conclusions from metacommunity models with high amounts of mixing among local sites is that the total species pool for the system as a whole will be reduced by this mixing, even though it might be predicted to be higher if mixing was reduced (Mouquet and Loreau 2002). This is a very difficult prediction to test, because these species are simply absent from the entire system, in contrast to the case for metacommunities with less mixing. In the case of *C. finmarchicus*, for example, it may be that other copepod species would exist or increase in the system in areas where *C. finmarchicus* is common as sink species, but this would be difficult to ascertain, especially the altered advection of these species is also to be accounted for. Nevertheless, this reduced functional diversity is one of the key elements in constraining the response of these ecosystems to environmental change via processes involving CAS. To date, evidence on the susceptibility of local ecosystems to local environmental change in these large water bodies is slight.

Of interest, however, large water body metacommunities may show as much or more idiosyncrasy as isolated lake-pond systems. For example, recent experiments in which iron was added to ocean ecosystems have shown heterogeneity in trophic-structure responses that is qualitatively similar to those observed in lake and pond ecosystems in which dispersal was absent or low (discussed above), with strong plant responses observed in some case and strong herbivore responses observed (or hypothesized) in others (*see* Boyd 2002 for a recent review). However, they have also shown some evidence for adaptive responses to some environmental change (e.g., Kerfoot et al. 1999). It is currently very difficult to assess whether the heterogeneity of responses seen in such systems is due to the metacommunity dynamics we have described in the present article. Nonetheless, the patterns suggest that this may warrant more thought.

In the present article, we have tried to draw attention to some of the ways in which limnologists and aquatic ecologists might consider how processes that occur at larger spatial scales alter dynamics and patterns of variation seen at the local scale. Our discussion has been highly speculative, but we have tried to draw as much attention as we could to current empirical and theoretical knowledge. These issues are not easy to study, and they will require innovative approaches to evaluate them. Especially challenging and useful, however, is the integration of insights that come from theoretical, experimental, and observational work done across a variety of systems. Here we have highlighted very broad contrasts among ponds, lakes, and large water bodies, but such broad and general contrasts are very limited in the insights that they allow into these issues. The insights are likely to be valid only at a very gross level, because the relationships among connectivity, dispersal, and environ-

mental change are only likely to be loosely linked to these somewhat arbitrary distinctions among ponds, lakes, and large water bodies. We feel however, that they serve to lay the groundwork for comparative studies into the dynamics of these systems and into better understanding how community processes at different spatial scales affects the emergent behavior of these important and dynamic ecosystems.

The major conclusion we advance as a speculation is that connectivity of local communities in aquatic metacommunities can explain a range of dynamic behaviors related to their capacity to respond “adaptively” to environmental change. Nascent theory on this issue indicates that such adaptive behavior should be most apparent at intermediate levels of connectivity. We have presented evidence that, for planktonic systems, this intermediate level of connectivity may be most apparent in some metacommunities such as ponds in wetlands. We also present evidence that this is less so in larger lakes (where connectivity seems to be substantially lower) and in large water bodies (where connectivity, in contrast, seems to be much higher). To date, evidence to confirm these speculations is far from conclusive. Nevertheless, the metacommunity perspective allows some important insights into ways of interpreting data on the dynamics of these ecosystems.

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