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## Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems

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**Abstract.** Explaining the mechanisms underlying patterns of species diversity and composition in riverine networks is challenging. Historically, community ecologists have conceived of communities as largely isolated entities and have focused on local environmental factors and interspecific interactions as the major forces determining species composition. However, stream ecologists have long embraced a multiscale approach to studying riverine ecosystems and have studied both local factors and larger-scale regional factors, such as dispersal and disturbance. River networks exhibit a dendritic spatial structure that can constrain aquatic organisms when their dispersal is influenced by or confined to the river network. We contend that the principles of metacommunity theory would help stream ecologists to understand how the complex spatial structure of river networks mediates the relative influences of local and regional control on species composition. From a basic ecological perspective, the concept is attractive because new evidence suggests that the importance of regional processes (dispersal) depends on spatial structure of habitat and on connection to the regional species pool. The role of local factors relative to regional factors will vary with spatial position in a river network. From an applied perspective, the long-standing view in ecology that local community composition is an indicator of habitat quality may not be uniformly applicable across a river network, but the strength of such bioassessment approaches probably will depend on spatial position in the network. The principles of metacommunity theory are broadly applicable across taxa and systems but seem of particular consequence to stream ecology given the unique spatial structure of riverine systems. By explicitly embracing processes at multiple spatial scales, metacommunity theory provides a foundation on which to build a richer understanding of stream communities.

**Key words:** biodiversity, dendritic ecological network, dispersal, drift, metacommunity ecology, patch dynamics.

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### Metacommunities and Ecological Networks

In recent years, the terms metacommunities and ecological networks have generated excitement and a flurry of new research, including some of the contributions in this special issue. Unfortunately, after an initial surge of enthusiasm, many new concepts fizzle as enthusiasm wanes under close scrutiny and the messy details of real-world application (Belovsky et al. 2004). So are ecological networks and their integration into metacommunity ecology more salesmanship than substance? What, if anything, can these ideas contribute to the study of streams and rivers?

We hope to demonstrate that ecological networks and the links with metacommunities are more than new buzzwords and that these concepts do have potential to generate novel insights into the structure and function of riverine populations, communities, and ecosystems. Recent reviews have provided the basic background and theory of metacommunity structure and dynamics (Leibold et al. 2004, Chase 2005, Holyoak et al. 2005a). Thus, rather than attempt to summarize a set of new publications in this rapidly developing field, we present the major concepts of metacommunity ecology to facilitate a discussion of why the framework may be of specific relevance to the study of riverine networks.

#### *The basics of metacommunity ecology*

Historically, community ecologists have focused primarily on the local scale (Leibold et al. 2004). Notable exceptions exist—for example, Island Biogeography Theory (MacArthur and Wilson 1967) and lottery models of community assembly (Sale 1977)—but the bulk of prior research in community ecology has been devoted to how species interactions and local environmental conditions dictate community structure and dynamics. This research produced many insights into the functioning of communities. Nevertheless, efforts to understand the principles controlling community structure and dynamics have often fallen short of describing the composition and dynamics of real communities (Leibold et al. 2004). One possible explanation for these shortcomings is that processes occurring at regional scales (rather than local scales) strongly influence community structure and function (Holyoak et al. 2005b) and these processes have been largely excluded from efforts to understand communities. Previous generations of ecologists have certainly recognized the potential importance of processes occurring at regional scales, but permeation of these ideas into ecological theory and practice has been painfully slow (Ricklefs 1987,

2008, Cornell and Lawton 1992). In response, the *metacommunity framework* formalizes a multiscale approach to the study of ecological communities (Leibold et al. 2004, Holyoak et al. 2005a), and this growing effort to include regional/geographic processes in explanations for the structure and functioning of communities has been called “...a major synthesis in ecology” (Ricklefs 2008).

A metacommunity is a set of local communities connected through the dispersal of multiple potentially interacting species (Leibold et al. 2004), and the central tenet of metacommunity theory is that the dynamics and structure of many communities cannot be understood by focusing exclusively on local-scale processes. Thus, the fundamentally unique characteristic of metacommunity theory is the simultaneous consideration of processes at multiple spatial scales. Metacommunity theory recognizes 2 general types of forces that can affect the structure of communities: *local* and *regional*. Local processes include species interactions and local environmental conditions. Regional processes relate primarily to the dispersal of organisms between local communities (Urban 2004, Holyoak et al. 2005b). These broad sets of processes interact to produce multiple types of community dynamics characterized by differing degrees of local and regional influence on community structure (Fig. 1). Within this framework, no tradeoff necessarily exists between local and regional influences on community structure. Instead, both local and regional processes can simultaneously and interactively influence communities (Fig. 1).

Disturbance is a key component of metacommunity theory (Chase et al. 2005) and can exert a major influence on community structure, particularly in riverine systems (Resh et al. 1988, Townsend 1989, Death and Winterbourn 1995, Matthaei and Townsend 2000). However, disturbance resists categorization as either a local or regional influence. The extent of disturbances may be large, suggesting that disturbance is a regional process, but widespread local variation in disturbance regimes is an important driver of differences among local communities (Urban 2004). Thus, disturbance can be viewed as operating locally or regionally depending on the degree of spatial autocorrelation in its intensity. This local variation in disturbance effects can lead to local variation among communities primarily because of a common tradeoff between adaptations that maximize fitness in competitive environments and adaptations to extreme environmental conditions (Connell 1978, Menge and Sutherland 1987, Wellborn et al. 1996, Collins 2000).

Other authors have distinguished several paradigms within prior research that fall under the

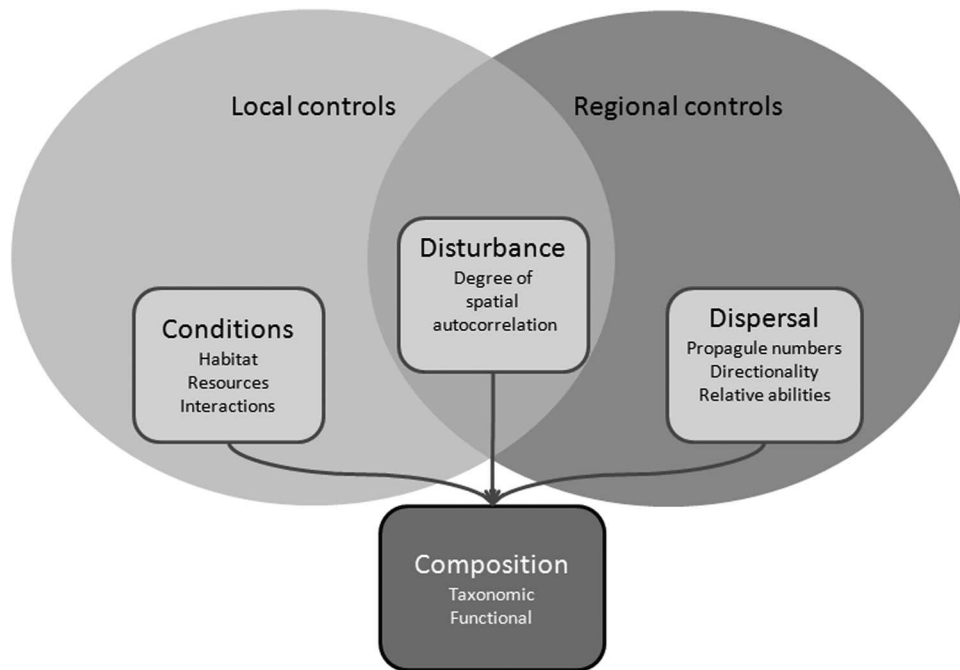


FIG. 1. Local controls (environmental conditions and species interactions) and regional controls (dispersal and landscape-scale extinction dynamics) interact to determine local community composition. Although local factors, such as the presence of particular geomorphic forms or water temperature ranges, may be usefully distinguished from regional factors, such as the number of natural or anthropogenic obstacles to movement, the metacommunity perspective emphasizes the need to study processes operating at multiple scales over efforts to categorize particular drivers as belonging to one scale or another. Rather than ask whether climate is a local or regional process, a metacommunity analysis seeks to identify how changes in precipitation could alter both the types of habitat available to a community and the nature of the linkages between those types.

general umbrella of *metacommunity*, including the neutral, species sorting, patch dynamics, and mass effects models (Leibold et al. 2004, Holyoak et al. 2005a). In the neutral paradigm, all species are functionally equivalent, and the dynamics of communities are dictated by loss (extinction, emigration) and gain (immigration, speciation) of individuals, with the dynamics of any particular species following a random walk. In the patch dynamics paradigm, all habitats are equivalent and can be occupied by members of the regional species pool, and local community composition is the product of extinction/colonization dynamics. The species sorting perspective emphasizes the sorting of species into the most appropriate habitat based on local environmental filters and species interactions and, thus, corresponds closely to the classic niche paradigm. In the mass effects paradigm, local environmental conditions and species interactions are potentially important, but high rates of dispersal can swamp local effects and allow species to persist in locations where they have poor competitive abilities. Disturbance plays a large role in many metacommunity paradigms, particularly patch dynamics and neutral theory, where it can be the force responsible for local

extirpation of species or individuals. These metacommunity paradigms can be represented within a framework similar to that illustrated in Fig. 1 that considers the relative degree of local and regional influence on community composition. All 4 listed paradigms address processes at multiple spatial scales, but they do not form the entire set of possible metacommunity models and are best thought of as specific instances of a more-generalized metacommunity framework (e.g., Fig. 1).

Numerous theoretical and empirical examples illustrate the utility of the metacommunity approach for simultaneous consideration of processes at multiple spatial scales. These examples come from a variety of organisms and systems including laboratory experiments (Cadotte 2006, Davies et al. 2009), mesocosm experiments (Howeth and Leibold 2010a), lakes (Beisner et al. 2006, McCauley et al. 2008), ponds (Cottenie and de Meester 2003, 2004, Urban 2004, Werner et al. 2007, Chase et al. 2009), coral reefs (MacNeil et al. 2009), forests (Jabot et al. 2008), grasslands (Cronin 2007), savannahs (Debout et al. 2009), agricultural landscapes (Driscoll and Lindenmayer 2009), and riverine systems (discussed below). However, despite several studies addressing meta-

community theory in riverine systems, its potential utility for the study of stream and river communities remains largely unrealized, perhaps because of several methodological and conceptual challenges outlined in the next section. These challenges could be viewed as opportunities to expand the field of metacommunity ecology and craft a broader framework that contributes to stream ecology.

### Challenges of Applying Metacommunity Theory to Stream Communities

River networks possess several features that differentiate them from the majority of systems previously considered under a metacommunity framework. Metacommunities usually are conceptualized as fairly discrete and well-defined local communities connected by dispersal, and most empirical research has been conducted in systems that generally conform to such a concept (e.g., ponds, treeholes, forest fragments). Several characteristics of riverine systems present challenges to the application of metacommunity theory. These characteristics provide opportunities for lotic ecology to expand metacommunity theory into a more flexible framework.

#### *River networks are inherently dendritic in structure*

Dendritic Ecological Networks (DENs) are unique in that they are linear, hierarchically branching structures. Habitat in a DEN is contiguous without the relatively discrete patches present in many other commonly studied systems (e.g., lakes/ponds, forest fragments, rock pools, experimental mesocosms). Instead, all of the branches and junctions of DENs are potential habitats (Grant et al. 2007).

#### *Dispersal of organisms is often strongly oriented*

Many stream-dwelling organisms respond to the bulk movement of flowing water by orienting their movement relative to flow (Skalski and Gilliam 2000, Lowe 2003, Petersen et al. 2004, Grant et al. 2009). Drifting macroinvertebrates move with flow; fish, salamanders, and the flying adult forms of many aquatic insects orient strongly upstream (Mackay 1992, Hershey et al. 1993, Macneale et al. 2004); and other organisms (e.g., blackflies) orient perpendicularly to flow when they disperse overland (Finn et al. 2006).

#### *Many organisms display extreme ontogenetic changes in their dispersal behaviors*

Ontogenetic change in dispersal behavior is particularly pervasive among stream insects. Aquatic larvae

disperse primarily through downstream drift, but adults may fly overland, frequently with an upstream bias (Otto 1971, Mackay 1992, Hershey et al. 1993, Macneale et al. 2004). Other organisms that display such shifts in dispersal behavior include salamanders (Grant et al. 2009) and fish (e.g., anadromous/catadromous species, Meka et al. 2003).

#### *Community definitions are often expansive*

The definition of *community* is always somewhat contingent upon a particular research question (Ricklefs 2008). In nonriverine systems, communities often are defined by a particular functional group or guild (e.g., grazers, predators, C3 grasses), or by type of organism (e.g., the zooplankton community, the plant community). On the other hand, many studies of stream communities are conducted on “the benthic macroinvertebrate community” which, by definition, is one of the most complex commonly researched communities. It typically includes hundreds of species,  $\geq 3$  trophic levels, complex trophic interactions, a variety of consumer types (e.g., shredders, herbivores, predators), and many species with complex life cycles.

### How Can Stream Ecology Benefit from Greater Incorporation of Metacommunity Theory?

The central tenet of metacommunity theory is the simultaneous consideration of multiple spatial scales. Thus, the metacommunity framework should prove useful given the evidence that multiscale processes are important in stream systems. The physical structure of watersheds creates linkages among spatial scales through the transport of organisms and materials (reviewed in Poole 2010). The life histories of many riverine organisms include dispersal behaviors that can span multiple spatial scales (Lowe 2009, Falke and Fausch 2010), and dispersal mechanisms can change ontogenetically (Mackay 1992, Grant et al. 2009). Applied riverine ecology, such as restoration and bioassessment, may also benefit heavily from a consideration of processes occurring at regional scales (discussed below).

What does it actually mean to consider riverine networks within a metacommunity framework? Figure 2 illustrates how processes occurring at multiple spatial scales within a watershed dictate the composition—and by extension, dynamics and functioning—of local communities. Benthic macroinvertebrates illustrate the important concepts in Fig. 2, but these same principles apply broadly to most stream communities irrespectively. The regional species pool (Fig. 2a) represents all organisms capable of partici-

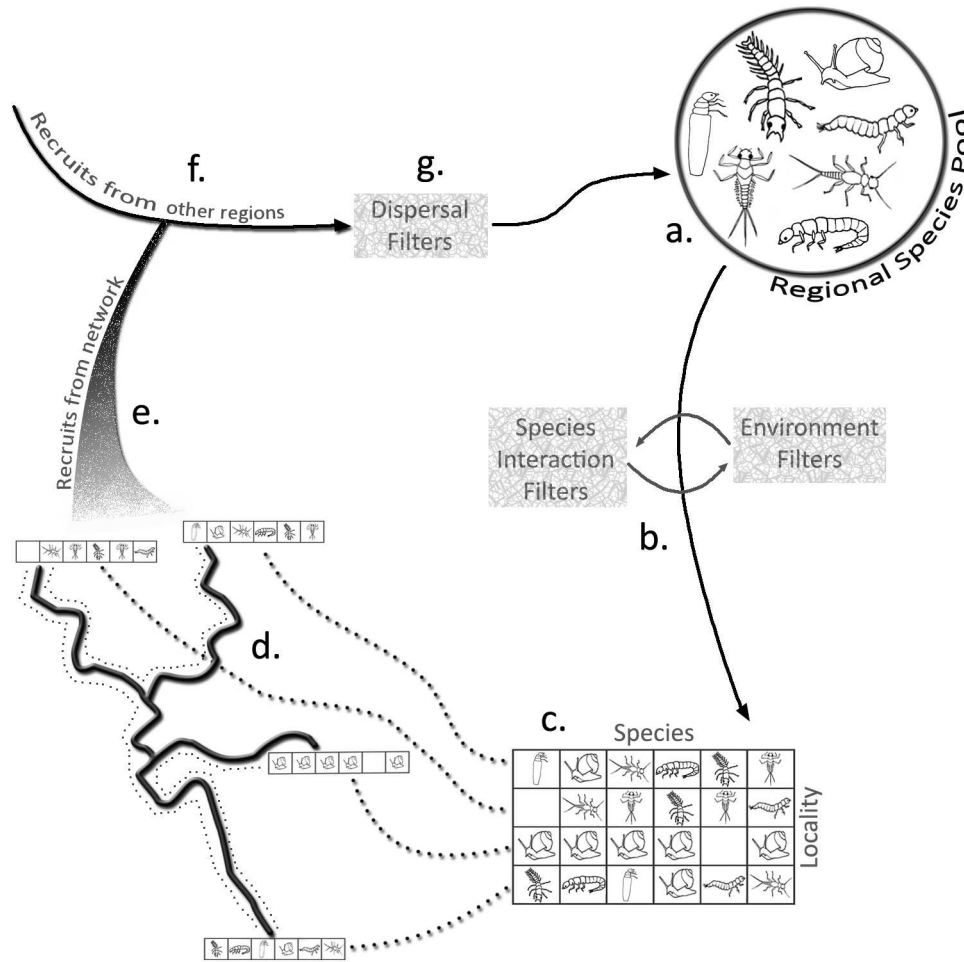


FIG. 2. Interactions between local (environmental conditions and species interactions) and regional factors (dispersal and landscape-scale extinction dynamics) in determining local community composition in riverine metacommunities. (a) The regional species pool represents the organisms available to occupy particular localities. (b) Organisms from the regional species pool are filtered based on environmental tolerances and species interactions into local communities. Grey arrows represent the necessary interaction between environmental factors and species interactions. (c) A local community can be defined as an assemblage of species within a particular habitat. In this case, each table cell is a microhabitat within a local community occupied by a particular species or left unoccupied (blank cells). (d) The riverine network. Large dotted lines illustrate the location of each local community in the habitat  $\times$  species matrix. Small dotted lines represent dispersal between local communities in the riverine network. (e) Dispersal of recruits into the regional species pool. This pathway includes both within-network dispersal (also illustrated by the small dotted lines in [d]) and out-of-network dispersal. (f) Recruits from other regions (i.e., neighboring riverine networks) that can potentially contribute to the regional species pool. (g) Dispersal filters, which are limits or barriers to the dispersal of organisms from a locality into the regional species pool. Filters may be particular to a species, or may affect any number of species. Benthic macroinvertebrate illustrations are courtesy of Laura E. Smith.

pating in a local community (c) at some point within the riverine network (d). Local forces—environmental tolerances and species interactions within a local habitat template—act as a filter (b) on the regional species pool so that, in most cases, the species at any locality (c) are a subset of the regional species pool (Poff 1997). Composition of local communities is certainly not fixed, and species within local communities can interact with one another through within-network dispersal (dotted lines in [d]). Ultimately,

organisms that successfully reproduce and send out recruits via within-network or out-of-network dispersal (e) can contribute to the regional species pool (a) along with possible recruits from adjacent regions (f). However, even after reproduction, contribution to the next generation is not guaranteed because the process of dispersal also filters (g) the organisms that will contribute to the regional species pool (a) and eventually to the next iteration of local communities (c + d).

Major abstractions in Fig. 2 are that the regional species pool is illustrated as a single entity, a sort of holding area distinct from the river network in space and time, and that the process of dispersal transports organisms to the regional pool. In reality, dispersal occurs continuously throughout the river network such that the portion of the regional pool that is actually available to colonize a local community varies with location. Furthermore, we illustrate processes in Fig. 2 as cyclical and ordered, whereas the dynamics of a metacommunity can occur simultaneously rather than as discrete steps, although the dispersal processes of some taxa could certainly be described as discrete and ordered.

Metacommunity theory as a unified framework has not been used extensively in stream ecology, but the recognition that local community composition is subject to the interaction between local environmental conditions (both biotic and abiotic) and dispersal-driven regional effects has a rich history in stream community ecology. Classic papers by Townsend (1989) and Poff (1997) and recent reviews by Winemiller et al. (2010) and Falke and Fausch (2010) discuss of the role of disturbance-mediated compositional turnover (patch dynamics) and hierarchical filters in community assembly and maintenance. The idea that position within a river network affects community composition also has old roots in stream ecology. Community composition has been proposed to vary predictably along the longitudinal axes of river networks (the River Continuum Concept) in response to predictable hydrologic, geomorphic, and resource (e.g., coarse particulate organic matter vs fine particulate organic matter) gradients (Vannote et al. 1980). In addition, disturbance regimes change predictably from smaller to larger reaches, and these changes are accompanied by concomitant changes in life-history strategies (Resh et al. 1988), which also may lead to transitions in predation pressure (Creed 2006). The constraints on local and regional processes imposed by hierarchically branching habitat (DENs) have recently emerged as an important area of research (reviewed by Grant et al. 2007). By dictating patterns of connectivity between local communities, the structure of DENs interacts with the dispersal of organisms to produce consequences for the persistence of metapopulations and recovery of local populations following disturbance that are not found in other ecological systems (Fagan 2002). This same dendritic structure is also proposed to contribute to the isolation of and differentiation between headwaters (Grant et al. 2007, Meyer et al. 2007).

#### *Existing contributions: metacommunities in river networks*

Several examples illustrate how the application of metacommunity theory has provided new insights into the effect of network configuration on community properties. Studies at large spatial scales have found that some fish-diversity patterns in the Mississippi–Missouri drainage could be modeled with only dispersal-driven (i.e., regional) processes (Muneepeerakul et al. 2008, Azaele et al. 2009, Convertino et al. 2009). In contrast, community composition of benthic macroinvertebrates (except for midge assemblages; Heino 2005) is strongly influenced by local environmental factors, particularly in headwaters (Heino and Mykrä 2008, Brown and Swan 2010, Patrick and Swan 2011). However, an investigation of the factors that structured macroinvertebrate communities in 10 New Zealand streams found that community structure was best explained by a combination of local and regional factors rather than by any set of processes individually (Thompson and Townsend 2006). An experimental study of the microbial composition of biofilms found that local habitat variables, particularly small-scale variance in flow regime and overall habitat heterogeneity, were good predictors of  $\beta$  diversity (Besemer et al. 2009). Landscape-scale survey data also suggest that stream bacteria are more heavily influenced by local habitat than by dispersal-driven processes (Finlay and Clarke 1999, Fenchel and Finlay 2004, Fierer et al. 2007).

The potentially strong influence of spatial structure on community composition arises from habitat isolation and habitat heterogeneity in headwater regions, and the increasing influence of dispersal as branches in DENs combine to form higher-order streams (Fagan 2002, Grant et al. 2007, Brown and Swan 2010). The accumulation of species and resources in nodes (confluences) of riverine networks also may strongly influence riverine communities. Earlier theoretical predictions of this pattern (Benda et al. 2004, Rice et al. 2006, Grant et al. 2007) have since been empirically demonstrated with fish assemblages (Kiffney et al. 2006, Hitt and Angermeier 2008a). The dendritic nature of river networks coupled with directional dispersal is also predicted to produce high  $\beta$  diversity (i.e., species turnover in space) in headwaters, but lower overall  $\alpha$  and  $\gamma$  diversity (i.e., local and regional diversity, respectively) for riparian plants (Muneepeerakul et al. 2007), and a review of diversity patterns in stream macroinvertebrates found similar effects (Clarke et al. 2008). However, in contrast to most previous studies, a recent investigation of macroinvertebrate communities in 8 Australian headwater streams partitioned diversity into  $\alpha$

and  $\beta$  components (sensu Jost 2007) and found that headwaters had low irreplaceability, i.e., they had high  $\alpha$  and low  $\beta$  diversity (Clarke et al. 2010). Furthermore, communities in different sections of DENs could be structured by dramatically different combinations of local and regional mechanisms despite being in the same watershed. Local environmental conditions dominate in headwaters, whereas a combination of local and regional processes dictates community dynamics in mainstems (Brown and Swan 2010).

*Using metacommunity theory to further applied research in riverine systems*

*Stream restoration: build it and they may not come.*—Stream restoration is increasingly used to mitigate the damage associated with a developing landscape. Restoration goals include, but are not limited to, reconnecting the active channel with the floodplain, increasing biodiversity, reducing sediment export, alleviating bank erosion, and increasing nutrient uptake. Restoration actions can range from soft methods like riparian replanting, to in-channel modifications (e.g., rock weirs) or, in many cases, reconstruction of entire channels. Whatever the method or goal, restoration is a purposeful manipulation of local conditions that influence the habitat features for stream communities. Restoration of biodiversity, be it richness or composition of key taxa (e.g., the Ephemeroptera, Plecoptera, and Trichoptera), may not be the primary goal in all restoration efforts, but diversity-based bioassessment techniques are often used to evaluate the success or failure of the activity. This measure of success reflects an implicit assumption that improvement of local habitat will lead to increased biodiversity. However, metacommunity theory suggests that relying solely on local habitat to increase biodiversity is unlikely to produce success in many scenarios.

Ecologists have called for integration of ecological theory with restoration practice (Palmer et al. 1997, Lake et al. 2007, Thompson and Lake 2010). Basic ecological theory suggests why many restoration efforts do not result in an improvement in the biological community. Palmer et al. (2010) reviewed studies that measured the relationship between biodiversity and stream habitat heterogeneity and found that increases in habitat heterogeneity did not result in an increase in biodiversity in the vast majority of studies of restoration projects, surveys, or experiments. The lack of a response of an ecological community to local conditions suggests a potentially important influence of regional factors, such as

dispersal, large-scale disturbance, and depletion of the regional species pool (Blakely et al. 2006, Palmer et al. 2010, Patrick and Swan 2011). Stream restoration practice might be an effective means by which to rebuild the local environment, but if done in the wrong regional context, a restored site may remain disconnected from the very organisms the restoration was meant to support. A consideration of the regional context, including effects created by the position of restored areas within a riverine network, may lead to more effective restoration practice that ultimately saves money and yields results that approach true restoration.

*Implications for bioassessment.*—Macroinvertebrates, fish, diatoms, and, to a lesser degree, amphibians have long been used as indicators of impairment in aquatic systems because they are sensitive to pollution, sedimentation, and other environmental changes. All bioassessment techniques rely on the ability to infer impairment based on the correspondence between the presence/absence of indicator species and measured or historical environmental conditions (Hawkins and Norris 2000). In bioassessment studies, target organisms and environmental conditions generally are measured on a local scale, even in assessments with a large spatial extent.

Could failure to consider dispersal-driven processes negatively affect the performance of bioassessment metrics? Regional dispersal reduces fish-metric sensitivity to local environmental quality and effectively reduces the influence of environmental factors on bioassessment metrics (Hitt and Angermeier 2008b, 2011). Moreover, chance dispersal events can contribute rare species to communities and their influence can be significant (Cao et al. 1998, 2001).  $\alpha$  diversity was controlled by environmental condition in a study of diversity patterns in plants, but  $\beta$  diversity was controlled by dispersal-driven differences in the regional species pool and was particularly influenced by rare long-distance dispersal events (Rajaniemi et al. 2006). Similar mechanisms could operate in river networks. Several stream-dwelling taxa undergo rare long-distance dispersal events (Macneale et al. 2005, Lowe 2009). The inclusion or omission of locally rare species in benthic macroinvertebrate-based bioassessments is still a matter of some debate (Cao et al. 1998, 2001, Cao and Williams 1999, Marchant 1999, Clarke and Murphy 2006, Van Sickle et al. 2007), and the recognition that many of those rare species might not be indicative of local environmental conditions adds an additional layer of complication.

*Regional dispersal mediates local effects of land use.*—In 1960, Hynes published *The Biology of Polluted Waters*. Since then, many pathways have been found by



which land use affects the biological structure and function of freshwater ecosystems. For instance, land use can affect organismal physiology directly (e.g., via riparian shade and water temperature) and indirectly through foodweb structure and competitive interactions (e.g., via nutrient enrichment). Land use has important consequences for stream community composition (Allan 2004) and bioassessment (Hughes et al. 2010). However, little of the substantial amount of work on dispersal that has been published in the last 50 y has been incorporated into the study of land use and stream biological integrity. We think that the emphasis on hierarchical spatial structure that is inherent to metacommunity principles may be a useful framework for understanding local and regional influences of land use on stream environmental quality.

In studies of local vs regional effects of anthropogenic land use in the watershed on stream communities, investigators often define regional variation in terms of extent of land cover types in the riparian zone or the watershed (Jones et al. 2001, Snyder et al. 2003, Frimpong et al. 2005). However, dispersal also may account for regional influences within and among streams. For instance, some stream fishes can move among connected streams (Gorman 1986, Osborne and Wiley 1992, Hitt and Angermeier 2008a, Thornbrugh and Gido 2010), so the spatial structure of dispersal within stream networks may mediate local effects of land use. Hitt and Angermeier (2008a, 2011) showed that relationships between local environmental stressors and composition of fish communities were weaker at sites flowing into mainstem rivers (basin area > 250 km<sup>2</sup>) than at sites that lacked riverine connectivity. If research were integrated across assemblages and dispersal strategies, the result might be a spatially hierarchical assessment of environmental quality because dispersal would be treated as a regional signal rather than local noise.

*Metacommunities and historical landuse change.*—Landuse changes can have dramatic, long-lasting effects on stream communities, and the type and intensity of these effects constantly change as human land use changes through time. For example, extensive abandonment of agricultural lands has occurred during the last century (Foster 1992, Flinn and Vellend 2005). Stream communities in historically agricultural watersheds are structurally and functionally different from those in nearby streams that were not disturbed by agricultural land uses (Harding et al. 1998, Maloney et al. 2008). Solid empirical data regarding the duration of landuse effects on stream communities are lacking, but metacommunity princi-

ples (e.g., extent of dispersal among communities) and techniques (e.g., graph theory, stream redundancy) should be useful when studies to gather such data are designed.

Longitudinal network position affects community structure (Huet 1959, Vannote et al. 1980), so it probably also affects community recovery. What are the implications for prospects of recovery following impairment or restoration actions if headwaters are more directly affected by conditions in the surrounding watershed (Brown and Swan 2010) and are more isolated than higher-order streams? Dispersal ability differs among the major taxonomic groups (e.g., invertebrates, fishes; Hughes 2007), so recovery is likely to vary among and within assemblages. Moreover, recolonization depends on the existence of source communities, so recovery will depend on variability in disturbance among the headwater watersheds. Strong spatial autocorrelation in damage across low-order basins should result in slow or nonexistent recolonization of damaged systems. Last, recently abandoned or restored systems offer opportunities to examine the relative roles of regional and local factors on stream communities. Many ecologists have attempted to dissect these 2 factors, and a study of recolonization dynamics in recently recovered sites may elucidate their relative roles (Patrick and Swan 2011).

*Design of freshwater reserves.*—Predictions derived from connectivity modeling have been used to improve the performance of marine protected areas (Botsford et al. 1997) and terrestrial reserves (Noss and Daly 2006). These predictions have rarely been considered in riverine conservation planning (Frissell and Bayles 1996, Herbert et al. 2007, but see Moilanen et al. 2008) even though dispersal and recolonization may be more sensitive to habitat fragmentation in stream networks than in terrestrial landscapes (Fagan 2002). This extra sensitivity may help explain why freshwater taxa exhibit higher extinction rates than terrestrial fauna (Ricciardi and Rasmussen 1999). Biological conservation in stream networks requires an understanding of regional dispersal (Fausch et al. 2002, Dudgeon 2006), and application of metacommunity theory could be beneficial in this regard. For example, metacommunity theory could improve freshwater reserve design for the US Wild and Scenic River system (i.e., from mainstems to stream networks), the US Endangered Species Act (i.e., designation of Critical Habitat networks for fishes), and the US Clean Water Act (i.e., Tier III stream designations).

*Climate change.*—Climate shifts are likely to offer the potential for new and interesting research on the factors that drive community composition in spatially

constrained environments. The effects of climate change on freshwater systems are expected to include increasing water temperature and a shift in hydrologic regime (Carpenter et al. 1992). Hydrologic regime influences the strength of local biotic interactions (McAuliffe 1984, Power et al. 1988) and community structure (Poff and Ward 1989). Changes in the frequency and intensity of precipitation will influence a myriad of local environmental factors important to stream organisms, such as local flow environment and substrate size distribution, both of which explain variation in local community composition and mediate biotic interactions (Cardinale et al. 2002). Rivers may become wider (or deeper in constrained channels) because of increased discharge (Carpenter et al. 1992). Increased width will open the canopy in formerly shaded reaches and could lead to increasingly autotrophic food webs with eventual consequences for grazers (Feminella and Hawkins 1995). Thus, warming is predicted to intensify interspecific interactions, particularly among ectothermic organisms (e.g., consumer–resource, predator–prey).

Species often are segregated longitudinally along the thermal gradient imposed by the stream network (i.e., cooler headwaters relative to warmer downstream reaches; e.g., Beauchamp and Ulyott 1932, Taniguchi et al. 1998). Regionally, warming is predicted to shift the geographic distribution of species by eliminating species from locations as their thermal tolerances are exceeded and by providing opportunity for species to move into formerly cooler environments (Beaumont et al. 2007, Williams et al. 2007, Deutsch et al. 2008). Such changes imply a shift in regional species pools that will affect riverine metacommunities. Although it is speculative, this example illustrates how the spatial structure of a river network could interact with climate change to influence competition and, thus, the strength of local effects.

### Questions and Directions for Future Research

Simultaneous consideration of processes at both local and regional scales could greatly benefit studies of aquatic communities in river networks. Below we briefly discuss several priority needs and potential directions for future research on riverine metacommunities.

#### *Defining scales: local vs regional and the regional species pool*

In a DEN, what defines local and regional communities? What are the spatial scales represented by *local*

and *regional*? Are these definitions conditional on the location of the community in the network? These questions are fundamental to the application of a metacommunity framework to stream research. Identification of the scales at which to consider communities should have a theoretical foundation. Unfortunately, in empirical community studies, appropriate spatial scales usually are dictated by logistical considerations, such as sampling effort or density of focal organisms, rather than theoretical considerations. Such constraints may limit our understanding of community and ecosystem processes because important phenomena probably are scale-dependent (Gaines and Bertness 1993, Fausch et al. 2002, Nathan et al. 2003). One solution might be to develop quantitative, spatially explicit tools to use the growing volume of data on stream community composition available from bioassessment efforts.

In theoretical investigations and empirical studies of other systems (e.g., ponds: Cottenie et al. 2003, pitcher plants: Kneitel and Miller 2003), translation of dispersal information into categorical determination of success/failure of dispersal among discrete patches has been fairly straightforward. In contrast, categorizing dispersal fate and identifying discrete local and regional scales is difficult and often arbitrary in DENs because they are inherently connected and continuous (Grant et al. 2007). The challenge of modeling and analyzing continuous processes in stream networks has so far received little attention. Anderson et al. (2006) discussed the importance of developing an understanding of continuous processes in river networks and outlined some tools that may lead to such understanding, including minimum habitat size and response lengths (Diehl et al. 2008), which measure the scale of effects of local disturbances (Anderson et al. 2006). Recent (and continuing) efforts to model the dynamics of open populations in strongly advective systems may help form the foundation for a true consideration of metacommunities in river networks where habitat is continuous (Anderson et al. 2005).

#### *Empirical studies of dispersal*

Empirical studies of dispersal provide critical information necessary to include dispersal-driven (regional) processes in stream community ecology. Predicting the role of dispersal-driven processes requires reasonable estimates of dispersal for a wide range of taxa under a wide range of conditions. A foundation of empirical dispersal studies (far too numerous to list here) already exists for a variety of riverine organisms including plants, fish, amphibians,

and both adult and juvenile phases of stream insects. We strongly encourage continued work directed at understanding the details of dispersal in DENs.

However, studying dispersal may be conceptually simple, but in practice, it can be quite difficult. Riverine communities are often speciose, and the dispersal characteristics of many organisms change with life-history stage, environmental conditions, or community composition. Climate and local environmental conditions affect the dispersal of some taxa (Petersen et al. 1999, Finn and Poff 2008), as does the behavior of other taxa within a community (Kohler and McPeck 1989).

Understanding the specific pathways used by a dispersing individual and the factors that affect these pathways is a complex problem. Clearly scale is a key consideration when characterizing movement distributions. However, heterogeneity in movement propensity, bias, and distance are common features of populations (Skalski and Gilliam 2000, Berendonk and Bonsall 2002, Cecala et al. 2009, Grant et al. in press), as is variation in life-history stage within (Bruce 1986, Labbe and Fausch 2000, Cecala et al. 2009, Grant et al. in press) and among species (Skalski and Gilliam 2000, Lowe et al. 2008, Berendonk et al. 2009). Our understanding of how heterogeneity in dispersal behavior may affect the dynamics of populations and how this may interact with the spatial structuring of real habitat networks often is based on theory without confirmation from empirical observations (MacDonald and Johnson 2001). Perhaps most vexing is the importance of difficult-to-observe dispersal phenomenon, especially rare long-distance dispersal (Nathan 2001, Trakhtenbrot et al. 2005, Lowe 2009). The sensitivity of some model predictions in habitat networks to the type and frequency of dispersal (Hill et al. 2002, Holland and Hastings 2008) underlines the importance of characterizing this trait to understand community dynamics.

A frequent problem when studying DENs is understanding how an organism chooses between 2 distinct dispersal pathways: within-network vs out-of-network (Macneale et al. 2005, Grant et al. 2007). Within-network dispersal follows habitat branches and may be a primary dispersal pathway and the only option available to species restricted to the aquatic habitat. However, the propensity for an individual to disperse overland (out-of-network) between habitat branches may be disproportionately important to population persistence (Fagan et al. 2010, Grant et al. in press). Topological complexity may interact with these dispersal behaviors and could lead to noninteracting subpopulations if dispersal is limited (Gilliam and Fraser 2001) or could affect metapopulation

persistence time if dispersal is biased (Grant 2011). Further isolation, especially if it limits rare (but important) dispersal events or restricts the use of certain dispersal pathways, may influence metacommunity patterns and dynamics. Developing expectations for population distribution and persistence and testing these expectations against field data may reveal important roles for specific dendritic network configurations and dispersal behavior in metacommunity models (Resetarits et al. 2005). Theoretical developments should focus on considering when space and topology matter (and when they can be ignored).

Theoretical and analytical tools can help to bridge the gap between empirical data and a more complete understanding of riverine systems. Empirical data can form the basis of modeled approximations using clearly articulated mathematical assumptions (e.g., exponential decay), which can in turn support model selection in analyses of distribution data. Species traits (Poff et al. 2006, Webb et al. 2010) also offer an opportunity to use data contained in detailed natural-history studies to generate generalizations for whole communities. Last, genetic methods are becoming increasingly affordable and field-friendly and can be used to elucidate dispersal patterns when field measurements prove impractical (Nathan 2001, Lowe and Allendorf 2010, Stutz et al. 2010).

#### *Partitioning local vs regional influences*

Distinguishing the contributions to community structure of local and regional factors is a central goal of metacommunity analyses. Categorizing these factors correctly is more than a simple intellectual exercise and can lead to critical information for management and restoration of natural systems (see *Application of spatial theory* below). Numerous empirical and analytical approaches can be used to differentiate between local and regional processes structuring communities. The most common approach is to analyze diversity patterns relative to spatial and environmental factors (Urban 2004, Heino 2005, 2008, Soinen et al. 2007, Hitt and Angermeier 2008a, Laliberté et al. 2009, Rominger et al. 2009, Brown and Swan 2010, Maloney et al. 2011). Other approaches include direct manipulation of local or regional forces (or both) in an experimental context (Kneitel and Miller 2003, Chase 2007, Belote et al. 2009, Chase et al. 2009, Howeth and Leibold 2010a, b) or inferential modeling approaches using existing data (Muneepeerakul et al. 2008, Azaele et al. 2009).

Some phenomena, such as disturbance and large-scale climatic events, resist categorization into local or

regional phenomena. In these cases, it may sometimes be more informative to identify the *effects*, rather than the phenomena themselves, as local and regional. If neither phenomena nor their effects can be categorized in any useful way, we stress that categorization is useful only if it leads to increased understanding of the structure and dynamics of communities. Thus, categorization should be viewed as a means rather than an end.

#### *Application of spatial theory*

A variety of methods exist that allow direct analysis of general properties of habitat networks and, therefore, straightforward comparisons of network properties within and among systems. These methods include simulation modeling (Labonne et al. 2008, Grant 2011), graph theory (Auerbach and Poff 2011), fractal analysis (Turcotte et al. 1998), geostatistical modeling (Peterson et al. 2007), hierarchy theory (Clauset et al. 2008), and approaches that combine elements of several methods (Rodriguez-Iturbe et al. 2009). In addition, authors of several studies have emphasized the importance of considering natural and manmade physical barriers in the analysis of habitat networks (Cote et al. 2009, Covich et al. 2009). Several methods hold potential for characterizing the relationships between portions of river networks. Here, we illustrate this potential with a brief description of the use of graph theory for this purpose.

Graph theory provides a set of tools for quantitative comparisons of the spatial template on which metacommunity dynamics occur (see Urban et al. 2009 for a review of landscape applications). Translating a continuous, often directional, ecological network into the edges and vertices of a graph demands careful attention to ensure that the representation is meaningful, the resulting data structure can serve as an object of analysis (Urban and Keitt 2001, Minor and Urban 2007) and as the basis for modeling dynamics (Schaefer and Kerfoot 2004, Auerbach and Poff 2011). Graph analysis makes it straightforward to measure properties of an entire metacommunity, such as the maximum and average path lengths between local communities, and various metrics for each local community, such as the size or character of its dispersal neighborhood or the total number of paths that traverse it. A graph can facilitate simulations that account for both local and regional processes by combining data in matrices that describe the attributes of a set of entities (e.g., a site  $\times$  species community matrix) with those that describe the connections between those entities (e.g., a geographical-informa-

tion-system-derived adjacency matrix). In general, such an approach involves updating the attribute matrix via functions that describe local interactions and functions that describe changes over the entire set of entities (i.e., immigration pressure based on the number of connected communities).

#### *Effects of network redundancy vs network heterogeneity*

Applications of metacommunity theory require new research to partition effects of dispersal from similarly sized and differently sized streams (i.e., network redundancy and heterogeneity, respectively). This distinction may be crucial for understanding the mechanisms of metacommunity processes because dispersal within redundant and heterogeneous networks may have different implications for taxonomic richness and community resiliency. Stream network heterogeneity increases local species richness at some spatial scales (Osborne and Wiley 1992, Hitt and Angermeier 2008a, 2011, Thornbrugh and Gido 2010), but stream network redundancy may be critical for recolonization dynamics (Brown and Kodric-Brown 1977, Fagan 2002) while having little effect on taxonomic richness. For example, the resiliency of salmonid populations in fire-dominated landscapes may be influenced by connectivity of multiple small streams (Dunham et al. 2003), and the resiliency of warmwater fish assemblages to stream drying may be influenced by the connectivity of multiple warmwater streams within a dispersal network (Magalhaes et al. 2002). In both cases, analysis of stream network heterogeneity alone would not predict significant effects on community composition, but regional dispersal could be crucial for community resiliency. The importance of stream network redundancy has been recognized for stream conservation (Frissell and Bayles 1996) and will be of increasing importance to predict stream community vulnerability to climate change.

### **Conclusion**

Metacommunity theory holds promise as a theoretical foundation to support future research in stream ecosystems. Elements of metacommunity theory already hold a prominent place in stream ecological research (e.g., the patch dynamics concept), but the spatial constraints imposed by and the advective nature of river networks call for embracing the many ways in which regional effects interact with local conditions to explain patterns in community composition. The contributions in this special series demonstrate clearly that stream networks cannot be viewed as offering the same level of local and regional

control on community composition across all systems. However, judging from the widespread use of techniques focused almost entirely on local environmental factors, the current practice of bioassessment implicitly downplays the importance of regional factors. Local community composition in spatially structured environments responds to gradients in local vs regional control. Given that human activities often change the spatial structure of stream networks, either directly (e.g., burying headwaters) or indirectly (e.g., climate change), scientists will be increasingly pressed to take a multiscale approach to understanding the mechanisms driving community composition in riverine ecosystems. By embracing a multiscale perspective, a metacommunity framework may help stream ecologists tackle new questions about stream communities and refine a variety of current management approaches.

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