Spatiotemporal controls of simulated metacommunity dynamics in dendritic networks

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Abstract. Understanding the mechanisms that create spatial and temporal patterns of functional diversity in stream networks is a goal of basic research and has implications for effective conservation of freshwater ecosystems. These patterns are likely to be influenced by the combination of temporally variable environmental conditions, movement constraints imposed by network structure, and the trait composition of local communities. We developed a simplified metacommunity model to investigate complex interactions among these factors under lottery competition for local resources, such as establishment sites. We used this model to examine how local and regional community composition varied in 3 scenarios: a null implementation involving only spatial effects, an implementation that combined network constraints with dispersal-trait variation, and an implementation in which a trade-off between multiple functional traits was paired with varying levels of temporal autocorrelation in the intensity of mortality. These simulations clarified the conditions that allow a single functional strategy to exclude others in a dendritic network and demonstrated 2 distinct modes of regional partitioning that can support the persistence of multiple functional strategies within such networks. The results suggested that the emergence of watershed or headwater–outlet partitioning depends on the functional dispersal differences present in the metacommunity and that autocorrelated mortality levels can collapse these regional divisions when they depend on a trade-off between dispersal ability and mortality resistance. We discuss the need to confront the complexity of interacting controls on community composition in rivers and streams and suggest opportunities to move beyond the basic framework we present.

Key words: metacommunity, functional diversity, dendritic ecological network, temporal heterogeneity.

Freshwater biotic communities are threatened by habitat loss, flow modification, and species introductions (Dudgeon et al. 2006, Poff et al. 2007, Rahel and Olden 2008). Designing conservation strategies that can respond adequately to these impacts requires an understanding of the biotic and abiotic forces that structure communities at multiple spatiotemporal scales (Townsend 1989, Poff 1997, Fausch et al. 2002, Thorp et al. 2006, Nel et al. 2009, Winemiller et al. 2010). Metacommunity theory is a promising framework for advancing this understanding because it integrates local, within-community mechanisms (e.g., species interactions) with regional, between-community ones (e.g., dispersal limitation, habitat turnover) as a set of hypotheses concerning the formation, maintenance, and alteration of diversity patterns (Leibold et al. 2004, Holyoak et al. 2005, Brown et al. 2011).

This growing body of theory is congruent with the conceptual development of lotic community and landscape ecology (Winemiller et al. 2010), but extending general metacommunity theory to rivers demands consideration of their defining characteristics. In particular, conceptual and evaluative models must account for flow directionality (Speirs and Gurney 2001, Lutscher et al. 2007, Muneepeerakul et al. 2008), dendritic network structure (Lowe et al. 2006, Campbell Grant et al. 2007, Muneepeerakul et al. 2007a, b, Brown and Swan 2010), and temporal environmental heterogeneity (Resh et al. 1988, Poff et al. 1997, Falke and Fausch 2010), all of which are known to influence the balance of local and regional mechanisms of community change (Poole 2002, Benda et al. 2004, Rodriguez-Iturbe et al. 2009).

Despite a number of important recent advances, a general understanding of the relationship between network-mediated dispersal limitation, temporal heterogeneity in environmental conditions, and the mode of local interspecific interaction remains elusive in

riverine ecosystems. Similarly, the consequences of the relationship between these factors for patterns of functional composition at multiple scales are not well characterized. Our goal was to illustrate some of the basic interactions between these mechanisms of community change as a step toward more predictive community ecology in rivers and streams.

We present results from a spatially explicit, discrete-time simulation model of local communities arrayed in dendritic networks and subject to temporally varying mortality levels. Individuals in the modeled metacommunity proceeded through a simplified life-history cycle involving lottery competition for available resources. Metacommunity members were assumed to belong to a single guild or trophic position, but they were potentially functionally distinct in terms of resistance to environmental mortality, dispersal ability, and other traits.

After a brief review of recent research concerning spatiotemporal controls on community structure in river networks, we describe this model structure in greater detail and present results from 3 tests of the model. As a null parameterization, we first examined how regional network configuration influenced communities subject only to compositional drift. We then explored how these spatial effects combined with variation in community members' dispersal capacity to alter regional composition. Last, we investigated how differences in the character of environmental variation interacted with these spatial- and functional-trait controls in a trait trade-off scenario. We conclude by considering some of the potential extensions and applications of this type of metacommunity approach to problems in riverine ecology and conservation.

Conceptual Background

A rich geomorphic literature examines and explains the drivers of variation in drainage network form (e.g., Rodriguez-Iturbe and Rinaldo 1997). Building on some of these concepts, ecological investigators have studied the ecological consequences of hierarchically branching riverine habitat. Theoretical work has demonstrated that channel configuration can influence movement rates (Johnson et al. 1995) and, thereby, predator–prey interactions (Cuddington and Yodzis 2002) and metapopulation dynamics (Fagan 2002, Lowe 2002, Labonne et al. 2009). Empirical work supports this general prediction and indicates that hierarchical branching structure affects local and regional drivers of community assembly (Honnay et al. 2001, Hitt and Angermeier 2008a, b, Brown and Swan 2010) and influences susceptibility to direct and indirect modes of habitat loss (Eikaas

and McIntosh 2006). Campbell Grant et al. (2007) reviewed much of this body of research in greater detail.

Dendritic structure also may factor into the evaluation of conservation strategies (Kuby et al. 2005, Schick and Lindley 2007). Extrapolating from models developed for salamanders and fish, Lowe (2002) and Fagan (2002), respectively, noted that movement restrictions related to dendritic network structure could have both beneficial (by reducing invasion speeds, buffering disease transmission, or creating spatial redundancy) and harmful (by reducing rescue effects or increasing proportional habitat loss from fragmentation events) effects on management targets. Falke and Fausch (2010) reviewed evidence of spatial effects on freshwater fish metapopulations and metacommunities. They noted that habitat configuration can play a particularly important role in determining the fitness of stream-dwelling organisms with ontogenically varying resource requirements (e.g., specialized spawning locations), and that regional dispersal limitation may vary with season and hydrologic circumstances.

Brown and Swan (2010) analyzed the similarity of stream macroinvertebrate communities in relation to dispersal constraints resulting from dendritic structure. By investigating the magnitude of distance–decay relationships (i.e., the shape of the curve describing between-site compositional similarity as a function of ecologically meaningful distance), these authors compared the relative importance of local niche-control and regional source–sink effects in headwater vs main-channel sites. They found support for their prediction that spatially isolated headwaters would be subject to greater niche control, whereas main-channel sites would show a greater influence of dispersal effects.

The importance of habitat configuration also has been examined via modeling. For example, in an analytical treatment of neutral metacommunities occupying various abstract topologies, Economo and Keitt (2008) observed that habitat networks with a more-restricted linkage structure produced greater overall diversity under reduced diversification rates. Muneepeerakul et al. (2007a, b) used a spatially realistic simulation approach to conduct a thorough theoretical analysis of equilibrium diversity patterns under both neutral and competition–colonization trade-off assumptions. They showed that, relative to a grid–lattice habitat configuration, dendritic structure consistently resulted in greater between-community (β) differences under both modes of local species interaction. However, trends in local (α) and regional (γ) diversity were more complicated and depended on

the type of interspecific interaction and the magnitude of directional dispersal.

Similar to the network-imposed diffusion limitation identified by Cuddington and Yodzis (2002), Muneepeerakul et al. (2007a, b) proposed a "containment effect", whereby dispersal restriction resulting from branching habitat structure facilitates the divergence of species composition in local assemblages and perhaps contributes to the relatively high species diversity in many river networks. In the models developed by Muneepeerakul et al. (2007a, b), this effect was generally exacerbated by the inclusion of strong downstream dispersal bias that rendered upstream sub-basins relatively inaccessible. These results appear to be congruent with theory addressing the drift paradox in ecosystems subjected to strongly advective dispersal. Lutscher et al. (2007) extended earlier single-population models (e.g., Speirs and Gurney 2001) to investigate the competitive implications of the relationship between downstream current velocity, population growth rate, upstream propagule diffusion, and total habitat dimensions. Lutscher et al. (2007) suggested the possibility of spatially mediated coexistence driven by the differences in species' combined capacities for growth and movement (i.e., reaction–diffusion) that produced what they termed "upstream invasion limits". The significance of such mechanisms in the larger context of dynamic drainage networks is an open question.

In addition to these indications of the importance of spatial configuration, many studies in lotic systems have demonstrated that altered environmental regimes can affect the fitness of individuals and, consequently, can shift community composition. Assemblages are thought to respond to changes in the periodic, stochastic, and catastrophic cycles of physical circumstances (i.e., variance in the frequency, magnitude, duration, timing, or rate of change of regimes of flow, temperature, sediment, etc.; Poff et al. 1997, Sabo and Post 2008). However, exactly how these responses occur in specific settings is often unclear because responses can be direct (physiological stress), resource-mediated (habitat loss/gain), or both, and can manifest at local or regional scales. For example, construction of a dam that reduces yearly flood peaks (a shift in magnitude in a periodic component of a flow regime) might locally alter riparian vegetation communities by favoring species with lower inundation tolerances (as reduced lateral connectivity increases their survival) and regionally by disfavoring hydrochoric obligates (as decreased travel distances diminish their dispersal kernel). Beyond these direct life-history effects, such a flow-regime shift could also affect communities by altering connections between habitat units (Merritt and Wohl 2006).

The effects of temporal environmental heterogeneity have received considerable attention in the theoretical literature concerning population and community processes (reviewed in Chesson 2000). This work has clearly established that, depending on the exact formulation of competitive interactions, environmental variation that influences demographic parameters can either stimulate competitive exclusion by perturbing a system away from a coexistence equilibrium or promote coexistence by preventing convergence to an exclusion equilibrium (e.g., Chesson and Warner 1981). Yet, to our knowledge, the critical characteristic of temporal variation in riverine systems has not been included in existing spatially explicit metacommunity models.

In an empirical study of the effects of disturbance on a lentic metacommunity, Urban (2004) concluded that temporal environmental heterogeneity strongly influenced numerous community attributes but interacted with spatial factors. On the basis of their empirical work, Falke and Fausch (2010) and Brown and Swan (2010) also suggested the importance of interacting spatial and temporal factors for explaining compositional dynamics. Theory confronting the interactions between dendritic structure and temporal heterogeneity is largely undeveloped, but a need for such research exists if we are to anticipate or respond successfully to changing flow regimes and drainage-network fragmentation. We developed our model as a contribution toward meeting this need.

Model Structure

Spatial configuration

We used a directed spatial graph to represent local communities (vertices) and the dispersal pathways assumed to connect them (edges). Spatial graphs and the broader set of tools associated with network analysis provide a convenient means of rendering the complexity of real landscapes in a conceptually and computationally tractable form (Newman 2003, Urban et al. 2009). The goal of our model development was to capture the important hydrogeomorphic and biological attributes of drainage networks as simply as possible.

The graphs forming the basis of the model can be interpreted in relation to a Strahler-ordered stream network (Fig. 1). The assumption that Strahler segments constitute an appropriate unit of habitat and that these habitat units correspond well to independent local communities linked by dispersal clearly depends on the taxa of interest. Post et al. (2006)
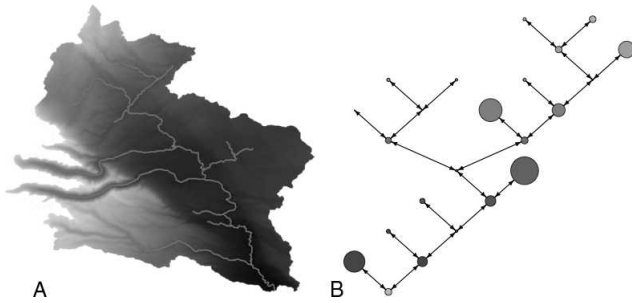
Fig. 1. A hydrologic network (A) can be rendered as the spatial graph (B). This type of graph translation captures planform topology and can represent characteristics such as reach length (shown here as vertex size) or the difficulty of moving between reaches (not shown; edge weight is uniform in this example). The edges in (B) indicate the type of simple bidirectional movement incorporated in all of the simulations described, although arbitrarily complex connections can be represented. Various alternative graphs could be derived from the same network depending on the question of interest, for instance treating junctions as vertices and reaches as edges. The graph layout and vertex shading in (B) are for plotting clarity and do not exactly correspond to the channel geography or relative elevation indicated in (A).

discussed the challenge of adequately matching biological and hydrogeomorphic boundaries, a special case of the complications inherent in the basic metacommunity assumption of discernible habitat patches and local communities (Leibold et al. 2004).

Nonetheless, the graph structure we used is a reasonable approximation of many real systems, particularly because of the scale-free topological properties of many drainage networks (Rodriguez-Iturbe and Rinaldo 1997). A similar graph might be abstracted from a coarser view of the channel network in which entire 3rd- or 4th-order catchments correspond to headwater vertices in the graph. Although the model dynamics can be extended to any empirically derived graph, we present results on a basic bifurcating tree structure for generality and clarity. All graph manipulations were performed with the igraph package (Csardi and Nepusz 2006) in R (version 2.8.1; R Development Core Team, Vienna, Austria).

After associating a Strahler order with the vertices representing local communities, we determined the maximum number of individuals that each local community could support by following the widely observed scaling properties of channel networks (Rodriguez-Iturbe and Rinaldo 1997, Dodds and Rothman 2000). Relative to 1st-order, or headwater, vertices with the capacity to support 500 individuals, we assigned the capacity of higher-order vertices as $500 \times R_L^{(\omega-1)}$, where ω is the Strahler order and R_L the

length ratio, which we set to 2 in accordance with various empirical estimates.

We represented the various environmental attributes affecting movement between communities (e.g., directional flow, stream power, natural obstacles) by assigning different weights to the directed edges linking graph vertices (edge direction indicates that the linkage between 2 vertices need not be symmetric). For this analysis, we limited the model to strictly in-channel linkages, but note that this approach is well suited to representing the out-of-channel movements that probably play an important role for many species with terrestrial or aerial life stages. The model can incorporate graphs with arbitrarily complicated movement pathways (i.e., every in/out edge having a unique value), but we focused on the broadly realistic cases in which downstream and upstream movements were considered collectively. Thus, the habitat units in the model differed only in size and accessibility resulting from network position.

Temporal heterogeneity

Identifying disturbance per se in the context of continually varying physical factors, such as discharge, temperature, and sediment load, presents challenges. The same environmental conditions may constitute disturbance in one spatiotemporal setting and the norm in another. However, an important distinguishing feature of disturbance is the mortality of individuals (Sousa 1984). Therefore, we represented the effects of temporal environmental heterogeneity at the regional scale as a generic index of environmental quality corresponding to the intensity of mortality, with values approaching 0 during high-mortality cycles and 1 during low-mortality cycles.

During each time step of a simulation run, each local community lost some percentage of its individuals as a function of the environmental-mortality index value (although we examined the effect of local variation in the mortality index, we present only results from runs in which all communities shared a single, regional value). The free capacity resulting from this mortality created the opportunity for competition in local communities. Individual survival was determined as a combination of the value of the environmental-quality index and the value of a parameter determining the ability to withstand the conditions leading to mortality. Thus, a metacommunity member with greater resistance (parameter value $\rightarrow 1$) during a cycle with conditions implying low overall mortality (environmental-quality index value $\rightarrow 1$) would have a high probability of surviving.

Although time series with various properties are possible, here we implemented 2 forms for the sequence of environmental-quality index values: random and autocorrelated. In random sequences, we varied the index value around some mean with no correlation from time step to time step (Fig. 2A). In the autocorrelated sequences, we varied the index around the same mean with the constraint that immediately proximate values were more similar to each other than to more temporally distant values (Fig. 2B, C).

We generated random and autocorrelated sequences as draws from a multivariate normal distribution with the number of variables equal to the number of time steps in a run. The covariance matrix was given, respectively, by an identity matrix and a matrix of negative-exponential-transformed Euclidean distances between variables (time steps) with a parameter (β) to adjust the degree of autocorrelation. We normalized the vector of values as $S(i) = e^{T(i)}/(1 + e^{T(i)})$, where $S(i)$ is a normalized sequence and $T(i)$ denotes the raw draws indexed by i. This method of synthesizing a time series controlled the mean and variance of values in the sequence and allowed discrimination of the effects of autocorrelation from other changes in the distribution of values.

Life-history events and community configuration

In contrast to models tracking binary occupancy probabilities, we choose to represent community change in terms of the relative abundances of community members to gain finer control of life-history events. For greater generality, we modeled the metacommunity in terms of several key functional traits that are likely to influence population, and hence, community dynamics in rivers and streams (Poff et al. 2006). Members of the metacommunity underwent a simplified sequence of life-history events during each time step of a model run. Mortality was imposed on local communities, the remaining populations reproduced, propagules were dispersed throughout the network, and populations were updated following the results of weighted establishment lotteries in each local community.

We chose this order of events for its conceptual clarity. It is appropriate for the many rivers with cyclical flood mortality in which organisms may time reproduction to take advantage of post-flood conditions (e.g., riparian seeds that settle on bare alluvium or fish that spawn in nutrient-rich or predator-free backwaters). We avoided stage structure for simplicity and based the model on the assumption that populations consisted only of reproductive adults and dispersing juveniles. We made the additional as-
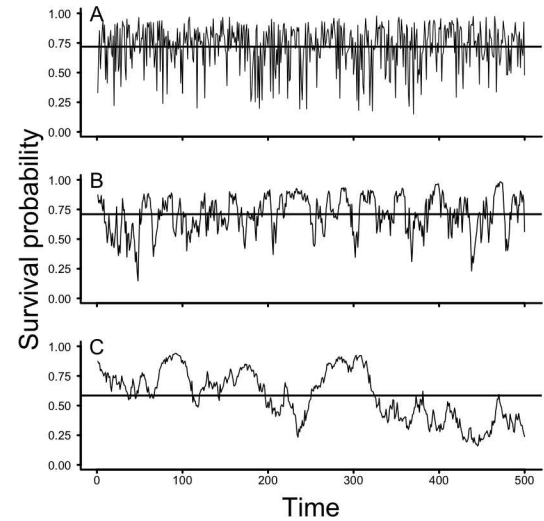

FIG. 2. Three example sequences of an environmental-quality index implying higher (values approaching 0) or lower (values approaching 1) community-wide mortality. The sequences illustrate different levels of temporal autocorrelation. A.—Mortality levels are independent from each time step to the next. B.—Mortality levels are somewhat autocorrelated ($\beta = 0.15$). C.—Mortality levels are strongly autocorrelated ($\beta = 0.025$). Horizontal lines indicate the sequence mean.

sumption that newly established individuals surviving to reproduce in the next time step were fully mature after 1 cycle. These assumptions are justifiable for rapidly maturing organisms and riverine systems that experience a high degree of population turnover, but we recognize that they are not representative of all competitive metacommunities, most obviously those including organisms whose reproduction is aperiodic or whose life histories involve prolonged lags between dispersal and reproductive maturity.

Differences in the parameter values used in the equations describing these processes created alternative functional strategies among metacommunity members. We recorded changes in the local and regional abundances of these different functional strategies in a local-community-by-strategy matrix $\mathbf{M}$, where element $\mathbf{M}(i,j)$ was the abundance of strategy j in local community i. During each time step, the survival of the population indexed by $\mathbf{M}(i,j)$ was simulated as draws from a binomially distributed random process, with the number of trials equal to the post-establishment population of strategy j in community i following the previous time step. The probability of survival was given by

$$p_{i,j,t}(survival) = S_t \times r_j$$

where $0 < r_j < 1$ is the resistance-trait value for

strategy j and $0 < S_t < 1$ is the temporally varying index corresponding to regionally favorable or unfavorable conditions (described above).

Following mortality, we calculated a 2nd community-by-strategy matrix **O** as the offspring produced by the survivors in **M**. Each $\mathbf{O}(i,j)$ was simulated as a random draw from a Poisson distribution, with λ set by

$$\lambda_{i,j}(offspring) = \mathbf{M}(i,j)f_j$$

where $0 < \sum_j \mathbf{M}(i,j) < capacity_i$ is the surviving population of individuals with strategy j in local community i, bounded by the total size of the community, and $0 < f_j < \infty$ is the value of the fecundity parameter for individuals with strategy j, corresponding to the per capita reproduction for individuals with that strategy. This functional form allowed for spatial variability in reproduction among communities (with variance increasing for larger populations or more-fecund strategies), but did not account for individual demographic variation within a strategy (reproductive output was pooled within strategies in each community). In addition, this formulation did not explicitly include any distance- or time-based dispersal mortality, so that the per capita reproduction parameter corresponded to the expectation of the distribution of offspring that survived to compete for establishment.

Following reproduction, dispersal acted to distribute offspring, generating a 3rd community-by-strategy matrix **P**, that represented the incoming propagule pool for each local community i. We used a set of community-by-community dispersal matrices $\mathbf{D}_j$ (one for each distinct dispersal strategy) to calculate the elements of matrix **P**. The rows of each $\mathbf{D}_j$ described the proportions of strategy j propagules in each community i that would reach all communities v (including i). Note that while all communities are technically accessible in a bifurcating graph, distant communities may have an essentially 0 chance of receiving propagules. The dispersal matrix proportions accounted for differences between communities in access to other neighboring communities, while ensuring that propagules with a particular strategy had the same underlying movement capacity throughout the network.

To construct each $\mathbf{D}_j$, we first described the maximum potential path weights k that could be traversed by propagules of strategy j with a discrete-probability density function given by:

$$\mathbf{P}(\text{propagule of } j \text{ traversing path weight} \leq k) = \frac{d_j^k}{\sum_k d_j^k}$$

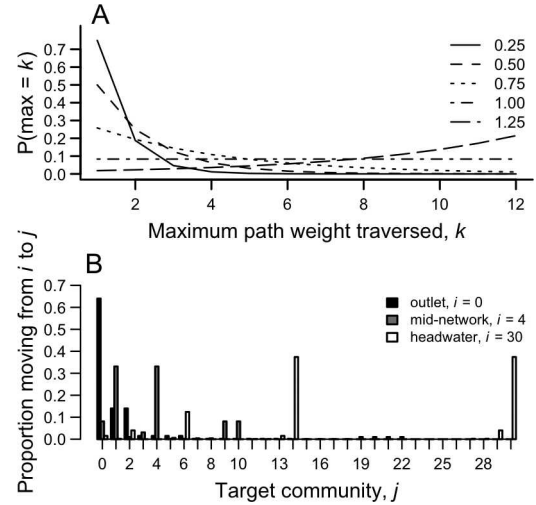where $0 < d_j < \infty$ is a dispersal parameter that sets the

FIG. 3. Functional dispersal differences in the model emerge from differences in the discrete movement kernels produced by a dispersal parameter (see text for details). This kernel describes the probability that a propagule will have a maximum movement ability of a path weight k, where path weight is the sum of the edge weights separating communities and corresponds to their effective distance. A.—Shape of distributions at different values of the dispersal parameter. Larger values increase the likelihood that a propagule of that strategy could reach a more distant community. These differences in dispersal ability were then translated into community-specific propagule proportions. B.—An example of the proportions moved from the outlet, a mid-network community, and a headwater community for a strategy with a dispersal-trait value = 0.5 under a downstream edge-weight bias (see text for description of alternative movement-bias scenarios). The index of receiving communities j increases with distance from the outlet, so that, for example, headwater community 30 has a direct downstream connection to community 14 and indirect connections to all others.

shape of the normalized power function (Fig. 3A) and k ranges from 1 to the largest path weight in the graph (smaller path weights are ecologically closer). We assumed that propagules leaving i could settle uniformly in any community along a path with a weight $\leq$ those propagules' particular maximum movement capacity. Thus, each $p_j(x = k)$ was divided by the total number of such neighboring communities ($x \leq k$) for that i to give the community-specific realized proportions of propagules that could move to neighbors k-distant. For example, the $p_j(x = k_{max,i})$ associated with the maximum path weight for a community was divided by the total number of communities because all of the available paths had weights $\leq k_{max,i}$ (such that the proportion reaching the most-distant neighbors would be very small).

The proportion of propagules contributed to each k-distant neighboring community was, therefore, assigned as the sum of the realized proportions moving k and all greater weights $\leq k_{max}$, (because of early settling of propagules capable of moving more than k), to form the rows of each community-by-community matrix $\mathbf{D}_j$. During each time step, the contribution of strategy j from a single local community i to all v was simulated as $\mathbf{O}(i,j)$ random draws from a multinomial distribution with class probabilities set by the community proportions in row i of $\mathbf{D}_j$ (draws were with replacement because communities were not used up as propagules move). Drawing across each strategy for all communities then filled $\mathbf{P}$.

We simulated establishment in local communities as simple weighted lottery competition (no dominance or interference effects were assumed among strategies). We determined the total number of propagules of any strategy that established in community i as the smaller of either the amount of free capacity in i or the total number of propagules in row i of $\mathbf{P}$. The total establishing individuals in i set the number of random draws from a multivariate hypergeometric (Wallenius noncentral) distribution with class probabilities corresponding to the proportion of each strategy j in the propagule pool for that community (draws were without replacement because propagules were used up as sites were filled). Last, we added these successful propagules to the surviving populations in $\mathbf{M}$, and the cycle repeated.

Simulation Results

We examined model behavior under alternative spatial structures, functional-trait compositions, and environmental-mortality regimes to clarify the conditions leading to 2 qualitatively distinct patterns: convergence to exclusion by a single functional strategy or the persistence of multiple functional strategies (to avoid confusion, we refrain from using the term "coexistence" to describe this outcome because of differences in its use; see Chesson 2000 for a detailed discussion of the various modes of and conditions for coexistence). Following initialization, patterns of metacommunity composition resulted from 3 basic processes in the model. First, mortality freed capacity. Second, stochastic (drift) and deterministic (dispersal capacity, mortality resistance) factors generated differences in the proportions of propagules entering establishment pools. Third, establishment fixed these proportional differences so that they carried through to the next cycle as differences in premortality abundance. Without these

proportional differences in the establishment pool, only stochasticity in the establishment process would alter relative abundances as a random walk.

The convergence to either exclusion or persistence of multiple strategies also was related to whether community members partitioned or failed to partition both local communities and the regional network. If the same winning functional strategy emerged deterministically in all communities or accelerating drift fixed the same local winner stochastically, then regional exclusion resulted. Alternatively, different strategies (trait-parameter values) could come to dominate their respective communities locally but lack the ability to invade all others, resulting in regional and, potentially, local persistence of multiple strategies via source–sink (mass effects) dynamics.

In accordance with previous theoretical studies of lottery competition (reviewed in Chesson 2000, Amarasekare 2003), exclusion in the model occurred in the absence of some type of spatiotemporal resource differences (i.e., some niche dimension to partition). Habitat units in the network varied only in terms of capacity (maximum local population size) and location, but multiple strategies could persist in the model despite this lack of variation in quality (e.g., differences in limiting nutrients). Our focus was on the mechanisms by which network structure, trait composition, and temporal heterogeneity created the conditions for this persistence. First, we describe how spatial partitioning can occur when ecological drift controls communities. Second, we examine how differences in dispersal ability can interact with network-mediated movement restrictions to generate an alternative form of partitioning. Last, we consider how changes in the sequence of environmental-quality values can alter the dynamics of a trade-off between dispersal ability and mortality resistance.

Unless otherwise indicated, we initialized all simulation runs with equal abundances of each strategy in every local community and, consequently, with equal regional proportions. Under some parameterizations, the model was sensitive to initial conditions (see below), but we chose to focus on the processes of maintenance and loss of diversity rather than on community assembly. Alternative initializations are possible but beyond the scope of our paper. For simplicity, in all model results described here, the fecundity-trait value (corresponding to per capita offspring surviving to establishment competition) was equalized at 100 for all metacommunity members. This value produced an excess of offspring relative to available capacity during each time step and prevented sampling bias associated with small populations. Thus, functional strategies were lost from the system

following competition, but the metacommunity as a whole never approached extinction.

The null case: ecological drift

The ability to observe dynamics while controlling sources of heterogeneity is a principle benefit of simulation. Therefore, we begin by describing the model's behavior when implemented without functional differences between metacommunity members. In this case, although the model tracks distinct populations, they share identical parameter values. This parameterization does not constitute a formal neutral model because neither speciation nor immigration supplied novel metacommunity members through time, but it indicated the patterns of community composition that would result if ecological drift predominated.

We examined the null case under 3 edge-weighting scenarios: downstream bias, upstream bias, and no bias. Directional dispersal influences diversity patterns in neutral dendritic metacommunities (Muneepeerakul et al. 2008) and in theoretical studies of 1-dimensional systems (Lutscher et al. 2007). Directional dispersal may combine with movement limitations caused by branching structure to influence community attributes, such as between-community compositional turnover (β-diversity). The no-bias scenario involved equal edge weights between all communities. We doubled the weights for edges moving away from and toward the outlet community to represent down- and upstream movement bias respectively. Total path weight, the sum of all edge weights between 2 communities, defined the effective distance between those communities and created network-mediated isolation. For example, with downstream bias, large path weights resulted either from separation by many downstream edges or a few upstream edges. The downstream scenario approximated primarily passive, with-the-current dispersal, whereas the upstream scenario more closely resembled active, against-the-current dispersal tendencies.

For all 3 edge-weighting scenarios, if the shared dispersal-trait value yielded a movement kernel with a sufficient degree of nonlocal dispersal, then the metacommunity experienced local and regional exclusion at a rate influenced by the overall level of environmentally induced mortality. Higher dispersal-trait values (strategies with greater movement ability) and lower environmental-quality values decreased the time to exclusion by producing greater population turnover and by providing surviving individuals with greater access to free capacity in more distant communities (d_j values $> \sim0.4$ produce kernels with

sufficient movement capacity; Fig. 3A, B [note that trait-parameter values are scaled for mathematical convenience]). This behavior was exactly as would be expected when functional equivalence leading to the loss of community members through drift is not balanced by the introduction of novel metacommunity members.

In contrast, the drift to regional exclusion can stall under a downstream bias if the metacommunity is composed of members with limited dispersal capacity because of a low, shared dispersal-trait value. When dispersal flux from neighboring communities fails to overcome stochastic fluctuations in local abundance, different strategies may come to dominate different local communities resulting in regional persistence of multiple functionally equivalent strategies. We termed this form of regional persistence "watershed-based" spatial partitioning of the network (illustrated in Fig. 4A for a 2-strategy case), whereby the combination of limited movement ability and network structure prevented the regionally dominant strategy from invading communities where this strategy was less common. A strategy with lower regional abundance could (numerically) dominate several headwater communities, resisting the incursion of other strategies because of a proportional advantage in nearby downstream lotteries. This advantage was generated and maintained by the relative ease of downstream movement and the identical, limited dispersal capacity of potential invaders.

The no-bias and upstream-bias edge-weighting scenarios precluded this outcome because propagule flux was dispersive rather than aggregative. The branching structure no longer allowed a strategy in the headwaters to balance the numerically dominant strategy's outward dispersal flux by combining propagules from several communities in downstream lotteries. Even when initialized so that 2 strategies each dominated the 2 major subwatersheds, the no- and upstream-bias scenarios allowed this partitioning to break down to regional exclusion (results not shown). Similarly, under a downstream bias and a higher shared dispersal-trait value, all strategies could send a significant portion of their offspring along paths with higher weights, and the directional advantage of dominating upstream communities was lost. Thus, the emergence of watershed partitioning in the null, downstream-bias scenario offered further confirmation of the potential importance of dendritic network structure as a source of isolation between communities (Muneepeerakul et al. 2008). Yet the breakdown of this partitioning with greater shared dispersal ability clearly demonstrated that branching structure alone is insufficient to produce
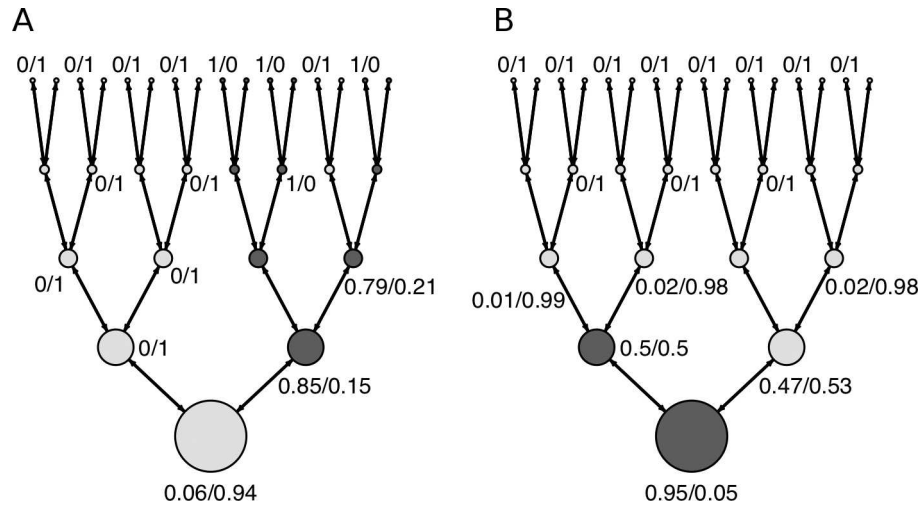
FIG. 4. Both panels depict metacommunities in which 2 competing functional strategies have stably partitioned the dendritic network. A.—Watershed partitioning resulted when directional movement bias and network structure combined to create isolation between communities, thereby allowing stochastic differences that emerged in the local abundance of functionally equivalent community members to persist as regional co-occurrence. B.—Headwater–outlet partitioning occurred when a strategy with primarily local dispersal dominated the outlet community while a strategy that moved more propagules over larger path weights dominated peripheral headwater communities. In both panels, the ratios beside selected vertices indicate the proportional abundance of each strategy in a community (following initialization of all communities at 0.5/0.5). Note that although most communities converge to exclusion by a single strategy, the regional persistence of both strategies in different communities supports a limited zone of local co-occurrence via mass effects.

the persistence of diversity in the absence of an interaction with organisms' movement limitations.

Variation within a single trait: dispersal differences

As expected, variation in parameter values for either the resistance- or fecundity-trait parameters alone produced a rapid deterministic convergence to exclusion (not shown). Simply by consistently having more propagules in lotteries, the functional strategy with the greatest reproductive capacity or the most resistance to mortality dominated, regardless of the movement bias or mode of temporal heterogeneity imposed. Variation in movement capacity was more complicated, however. The regionally dominant dispersal-trait strategy was dependent on both the edge-weighting scenario and the initial metacommunity composition.

When edges were weighted to produce upstream or a lack of movement bias, a single strategy consistently became regionally dominant. The strategy with the greatest degree of local dispersal excluded all others if the metacommunity was initialized with equal abundances. Such a strategy secured a numerical advantage in establishment lotteries throughout the network by retaining a greater proportion of its propagules in the communities where they were produced. Spatial variation in community capacity

also played a role in this outcome. Even if the locally dispersing strategy was initialized at lower abundances in all communities other than the outlet, it could eventually exclude other strategies. The large capacity of the outlet community served as a source for many propagules of the mostly local disperser, and without a movement bias that disfavored movement away from the outlet, these offspring could access upstream communities in sufficient quantities to win lotteries. The predominantly locally dispersing strategy failed to dominate regionally only if it began at a numerical disadvantage in all lotteries.

The advantage of concentrating dispersal locally is perhaps counterintuitive given the expectation that species should invest in dispersal even at considerable costs. In general, greater dispersal ability could benefit an organism if it increased access to new habitat for colonization or increased rescue effects following extirpation without incurring other fitness costs. Nonetheless, this aspect of the model's behavior followed logically from the lottery assumption and the upstream- and nonbiased-movement configurations. Success in establishment lotteries followed directly from relative abundance in the candidate pool, so small numbers of propagules from an invading strategy could not increase because of the absence of dominance or interference competition. Given a finite number of dispersers, those moving to

neighboring communities could not contribute to the local establishment pool and were usually at a numerical disadvantage in the communities where they settled. Even in the absence of an explicitly modeled Allee effect, if the number of dispersing propagules reaching neighboring communities subject to lottery competition is small relative to the number of locally produced propagules, then this dispersal will, at best, support a sink population and may reduce a natal relative advantage without securing any new territory. Despite this effect, the model also illustrated that strongly local dispersal is not uniformly advantageous. Network structure can combine with trait composition to create sufficient isolation to prevent a predominantly locally dispersing strategy from eventually taking over communities where it is less abundant.

A downstream edge-weighting bias can produce such circumstances. If a metacommunity initialized with equal abundances of 2 strategies throughout the network included an intermediate strategy that balanced local propagule retention with movements over larger effective distances, then this strategy could exclude either a competitor with predominantly local movement or one with a high proportion of movements over larger path weights. Such an intermediate strategy excluded the limited-movement strategy by more ably accessing free capacity in the early lotteries of enough distant upstream communities to use the total propagule advantage it thereby gained to eliminate the limited-movement strategy from the larger outlet and near-outlet communities. The reverse occurred in competition with the more mobile strategy. In this case, the intermediate strategy quickly dominated the larger downstream communities because of its greater propagule retention, but maintained sufficient movement ability to invade and dominate the fewer upstream communities in which the highly mobile strategy had gained an early local abundance advantage.

In contrast, a metacommunity consisting of the 2 opposing movement strategies could stabilize with both present. This outcome occurred when a locally moving strategy became dominant in the outlet and near-outlet communities, while the strategy with greater movement capacity dominated the headwater and mid-network communities (Fig. 4B). Such spatial partitioning was distinct from the watershed partitioning described for the null implementation and resulted from countervailing lottery advantages. The strategy with the ability to move propagules to distant headwater communities (i.e., those on paths with larger weights because of the downstream bias) experienced less competition for free capacity in the

upper than in the lower portion of the network. Simultaneously, the strategy with greater local propagule retention quickly gained a numerical advantage in the outlet. The combination of downstream bias and this strategy's movement tendencies prevented it from invading the upper portions of the network, yet it maintained local dominance in the lower communities because the capacity of the outlet community supported a sufficiently large population to balance the influx of invading propagules from upstream communities.

If both of these strategies were present in a multimember metacommunity, they could exclude the intermediate, balanced strategy and stably partition the network between near-outlet and near-headwater communities as in pairwise competition. Under these circumstances, the high- and low-movement capacity strategies prevailed in local lotteries in the portions of the network where each was favored (limited movement in the outlet, highly mobile in the headwaters), so that the intermediate strategy was at a disadvantage in all communities.

A functional trade-off: the impact of autocorrelated mortality

The sequence of environmental-quality index values controlled the overall rate of population turnover and, hence, the number of cycles to convergence for both the null and dispersal-variation configurations under all 3 movement-bias scenarios (higher mean mortality led to faster convergence). The form of temporal heterogeneity (either random or autocorrelated), however, did not alter the qualitative outcome of exclusion or partitioning in these two configurations. The model was also qualitatively insensitive to the form of temporal heterogeneity when strategies differed only in terms of the resistance parameter because the most resistant strategy maintained a consistent advantage.

The resistance-trait parameter exerted a linear effect on population differences because individual mortality was determined simply as a function of the per-time-step quality-index value multiplied by the strategy-specific resistance-trait value (see model description above). Consequently, the relative advantage associated with a superior resistance value was greatest when the index value was high (good conditions; values approaching 1), and this advantage was progressively reduced as the baseline mortality increased with lower-quality conditions. This functional form implies that organisms' behavioral and physiological adaptations to disturbance mortality are less effective as the intensity of disturbance increases.

At very high mortality (poor conditions), more resistant strategies were only marginally more likely to experience a lottery advantage. A combination of persistently low index values (consistently high-mortality cycles) and limiting similarity in the resistance parameter values could subject the system to drift rather than to deterministic control. We avoided this situation by setting all means for the environmental-quality sequences to 0.75, a level at which functional differences in the resistance parameter were clearly expressed.

In parameterizations that included variation in only the dispersal parameter, neither upstream nor non-biased edge-weighting scenarios yielded persistence of multiple strategies via headwater–outlet partitioning described above. Therefore, we focused on networks implemented with a downstream movement bias when investigating a dispersal-resistance trade-off. Under this condition (where upstream movement was more difficult than downstream), a trade-off between superior dispersal-trait values and superior resistance-trait values yielded a metacommunity that was qualitatively sensitive to the form of temporal heterogeneity.

To illustrate this outcome, we constructed a metacommunity composed of a strategy with limited-movement capacity but greater mortality resistance ($d = 0.4$, $r = 0.9$) and a strategy with greater movement capacity but increased susceptibility to environmental mortality ($d = 0.9$, $r = 0.83$). These parameter values enabled each strategy to exclude the other in the absence of the trade-off, under either form of temporal heterogeneity. Including these compensating trait parameters allowed a random (i.e., independent between time steps) sequence of environmental-quality index values to support stable regional partitioning following initialization at equal abundance throughout the network. With the 1st strategy occupying outlet and near-outlet communities while the 2nd dominated the remaining communities (Fig. 4B), this partitioning emerged according to dynamics similar to those described previously (Fig. 5A). The random variation in mortality levels from cycle to cycle favored neither strategy.

In contrast, a temporally autocorrelated sequence with similar mean and variance to the random sequence often resulted in the collapse of this partition or its failure to emerge (Fig. 5B). Furthermore, if the metacommunity first experienced a random sequence of environmental-quality index values that generated a stable headwater–outlet partition, but then experienced a shift to autocorrelated values, a similar collapse could occur (Fig. 5C). These outcomes were driven by shifts in the relative advantage conferred to each strategy by high or low index values. At the low index values corresponding to a harsh environment, the 1st strategy's relative advantage in mortality resistance was reduced, and the 2nd strategy was favored because of its greater dispersal ability. Conversely, consistently higher index values favored the 1st, more-resistant strategy because of its relatively greater post-mortality abundance.

Random transitions between high, low, and intermediate index values ensured that neither strategy could dominate lotteries for more than a few cycles. With temporal autocorrelation, the increased likelihood of similar values in succession meant that one or the other strategy might be favored over several subsequent cycles. Accordingly, the likelihood of the collapse to exclusion was proportional to the degree of autocorrelation (Fig. 6). Mortality sequences with longer durations of similar survival probabilities produced exclusion more frequently.

Discussion

This work is a first attempt to examine the combined effects of spatially explicit dendritic network structure and patterns of temporal variation on competitive metacommunity dynamics. Our simulation results demonstrate: 1) that network structure may support functional diversity by imposing movement limitations within a set of differently sized communities, but 2) that the influence of dendritic form depends on its interaction with individuals' movement ability and the directionality of movements, and 3) that autocorrelation in temporal environmental heterogeneity may reduce diversity if it destabilizes an otherwise-balanced competitive trade-off (Table 1).

When functional variation in movement ability was included, the model produced patterns of network partitioning that were congruent with previous theoretical work indicating that containment effects (Muneepeerakul et al. 2007b) or invasion limits (Lutscher et al. 2007) may contribute to coexistence at regional scales. In the terminology of metacommunity theory (Leibold et al. 2004), the model supported local species sorting based purely on network configuration and functional dispersal differences rather than on any variation in resource quality. Mass effects could also create a mid-network zone of local co-occurrence where communities operated simultaneously as sinks for strategies with headwater and near-outlet source populations. Overall, the model dynamics reinforce the importance of considering functional-trait differences, dispersal opportunities,
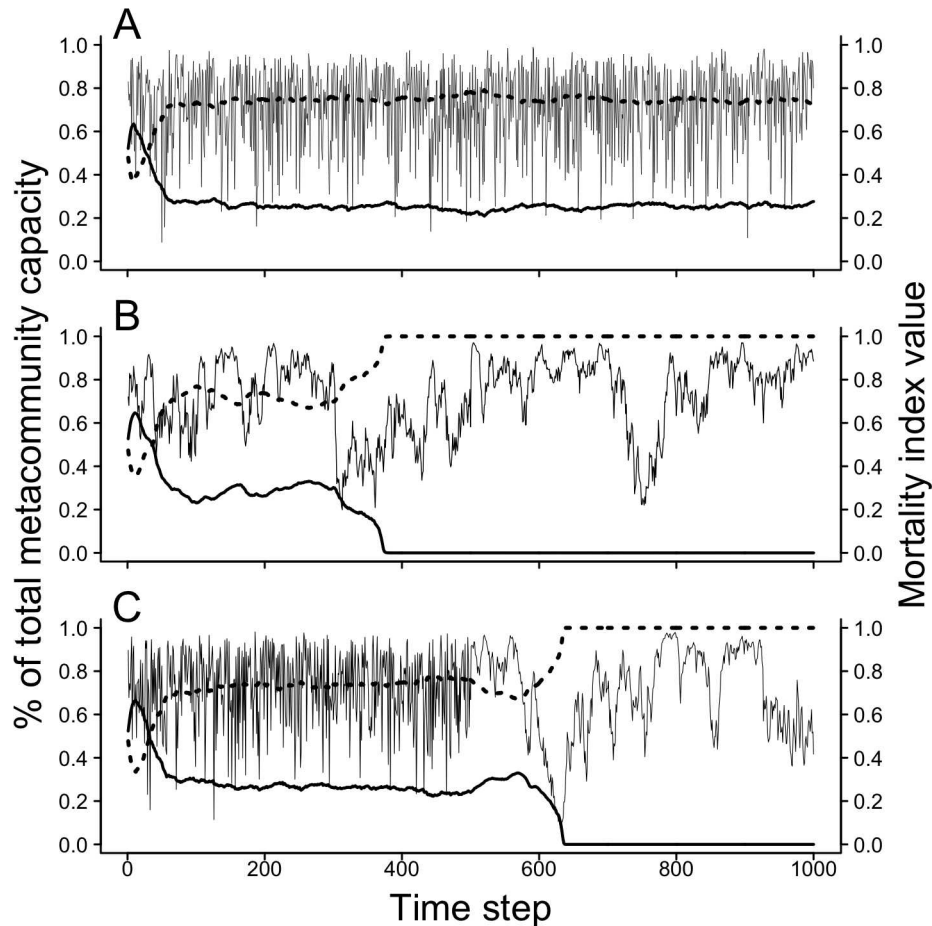
FIG. 5.   A.—In a metacommunity consisting of 2 strategies that trade-off dispersal and resistance, headwater–outlet network partitioning allows both to persist stably under a random sequence of environmental-quality index values. B.—Autocorrelated regional mortality levels can collapse this partitioning from an initialization at equal abundances. C.—Autocorrelated regional mortality levels can also collapse this partitioning if the network transitions out of a temporal regime in which independent mortality index values have allowed a partition to be established. The heavy solid and dotted lines represent the proportional regional abundances of each strategy, and the lighter gray lines indicate the environmental-mortality index value during each time step.

and environmental regimes in addition to local resource availability when studying or managing natural metacommunities.

Although the model's simplifying assumptions are not unreasonable for hierarchically branching river networks with increasing downstream community size and temporally varying mortality leading to scramble competition, they clearly limit its direct applicability. A simulation approach such as ours can yield useful insight into the mechanisms at work in multicausal systems by requiring the explicit articulation of assumptions and by making possible otherwise-difficult manipulation and replication. While our results provide some indication of a system's behavior if network architecture, temporal autocorrelation in environmental mortality, and the

included life-history traits were the primary axes of variation, metacommunity dynamics in the flora and fauna of river networks are likely to involve greater complexity in the form of factors, such as dominance competition, ontogenic niche shifts, evolving traits, and dynamic habitat templates.

The model incorporates only a single aspect of the many ways in which environmental conditions may change through time, and much work remains to identify which changes to the characteristic sequences of conditions are mostly likely to alter metacommunity dynamics. The science of environmental flows has advanced considerably in the last decade (see Poff et al. 2010 for a recent review), but linking specific elements of a hydrograph to the life-history transitions shared by multiple members of functional-trait
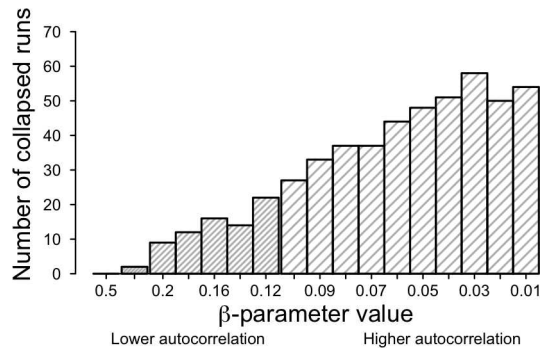
FIG. 6. Results after 500 time steps of 100 replicate runs initialized from an already partitioned network then subjected to unique mortality index sequences at varying levels of autocorrelation. Lower β-values correspond to increased autocorrelation, and a value of 0.5 generates a sequence that is nearly indistinguishable from random in terms of metacommunity behavior. Increasing autocorrelation increases the number of runs that collapse to exclusion because of the longer duration of periods with similar mortality levels that favor 1 strategy. Note that even relatively high levels of autocorrelation do not guarantee the occurrence of such a period within a particular environmental-quality index time series. See text for full details of model implementation.

communities is still a vital research frontier (Lytle and Poff 2004, Poff and Zimmerman 2010). For example, clarifying how an increase in the frequency of low-survival years interacts with dispersal opportunities to shift the balance among members of a metacommunity could have direct implications for how dam managers implement flow releases to benefit threatened native fish species or how regional water development is planned under climate-change projections. Although the goal of the work presented here was not the detailed model structure that such an application demands, it begins to indicate the value of a metacommunity perspective for explaining species abundance and distribution in management contexts. In combination with empirical data concerning the functional capabilities of taxa of interest, extensions of this type of simulation tool could prove to be valuable in scenario evaluation.

We assumed static network architecture to simplify our interpretation of the system's behavior, but the naturally dynamic habitat template and ongoing anthropogenic modification of rivers make relaxing this assumption a priority. Preliminary work testing the effect of network fragmentation by removing edges from simulations indicated that the direction and magnitude of metacommunity response is likely to vary with the type of functional interaction in local communities (e.g., null vs trade-off), as well as with

the location and number of lost dispersal pathways, and the pattern of temporal controls on resource turnover. From a management perspective, inadvertent or intentional human-assisted propagule movement may be of considerable importance in some situations. The graph-based structure underlying the model's life-history dynamics is quite flexible and could provide a useful platform for studies addressing the alteration of habitat units and the dispersal corridors linking them.

Further research into exactly how a spatially driven extinction debt (Tilman et al. 1994) manifests in dendritic structure may prove to be critical to assessing the vulnerability of metacommunity diversity to fragmentation and habitat loss. Conservation applications of network-scale community ecology are the subject of important current research (Minor and Urban 2007, 2008, Brooks et al. 2008, Ferrari and Lookingbill 2008, McRae et al. 2008, Pinto and Keitt 2009, Urban et al. 2009), and freshwater systems are receiving increasing attention (Lowe et al. 2006, Schick and Lindley 2007, Hitt and Angermeier 2008b, Moilanen et al. 2008). In general, better information about the network properties that predispose metacommunities to maintain functional diversity could significantly improve the process of planning protected freshwater areas (Saunders et al. 2002, Moilanen et al. 2008, Nel et al. 2009).

Future development also could examine the influence of extrinsic spatiotemporal forces in combination with more complex forms of population renewal and community interaction. Alternative modes of density dependence, Allee effects, stage-structured populations, and increased demographic stochasticity (i.e., individual variance in parameter values within a strategy) all are probably relevant to riverine metacommunity dynamics. Proportionally weighted lottery competition has the advantage of conceptual clarity, but some degree of dominance competition within the establishment process seems plausible for many natural metacommunities. Furthermore, when the simulation dynamics are viewed from an evolutionary perspective, it seems reasonable that selective pressure would modify the functional-trait values of co-occurring strategies and, thus, alter outcomes (Urban and Skelly 2006, Broennimann et al. 2007, Pearman et al. 2008). Allowing trait-parameter values to shift with time could facilitate examination of coupled evolutionary–ecological dynamics, a critical area of research for managers tasked with protecting assemblages expected to experience novel environmental regimes. Extending this framework to include greater trophic complexity, e.g., intraguild predation or the addition of consumer–resource relationships,

| Metacommunity composition | Edge-weight bias | | |
	Downstream	None	Upstream
Null implementation: no differences in trait values	All community members share a high dispersal-trait value: regional exclusion by random strategy, as stochastic fluctuations in local abundance are not reinforced All community members share a low dispersal-trait value: stable watershed partitioning possible as network-mediated isolation reinforces stochastic fluctuations in local abundance	Regional exclusion by random strategy	Regional exclusion by random strategy
Dispersal-trait variation only	Pairwise: community member with intermediate dispersal strategy (balancing local and higher path weight movements) excludes those with both predominantly local and predominantly non-local movement ability Multi-strategy: both regional exclusion of high/low dispersal parameter strategies by the intermediate strategy and exclusion of the intermediate as the high/low strategies stably partition the network into areas of local exclusion are possible	Regional exclusion by strategy with greater proportion of local dispersal	Regional exclusion by strategy with greater proportion of local dispersal
Resistance-dispersal trade-off	Random: supports partitioning and co-occurrence Autocorrelated: can collapse partitioning, especially as duration of similar values increases	Not evaluated	

could also improve the relationship of this type of model to particular functional metacommunities and increase the relevance of model outcomes to applied problems.

We examined shifts in functional diversity relative to a fixed regional pool of community members, but the exclusion or co-occurrence of life-history strategies are aspects of the more-general concern of biotic homogenization (Olden and Poff 2003). Addressing homogenization in lotic metacommunities entails representation of both losses and additions of community members. Our model results suggest that the regional success of invading organisms is likely to be mediated by the configuration of local community capacity and dispersal connections, as well as the properties of the temporal environmental regime that affect life-history transitions. Does an increase in the characteristic isolation of a network of communities (i.e., longer average path lengths) imply slower invasions by superior organisms or more rapid extinctions of endangered species? If so, how might the effects vary as, for example, the locus of introduction changes from headwater to mid-network to outlet communities, or if downstream dispersal bias does not apply to the system? The model behavior suggests that a novel, functionally superior strategy introduced downstream and at low abundance within a metacommunity experiencing relatively low overall mortality might have delayed or suppressed effects caused by the limited availability

of free capacity and the mass effects of incoming propagules from many upstream communities. This type of scenario merely illustrates how ignoring the complexity of multiple drivers of community change operating across scales risks the success of freshwater conservation efforts at the riverscape scale.

We hope that the questions raised by our work provoke greater interest in research that addresses the intersection of spatial habitat structure, environmental regimes, and the functional relationships between community members. This model represents a step toward a richer mechanistic understanding of the interactions between these factors and reveals several priorities for further development. We reiterate the call by Rodriguez-Iturbe et al. (2009) for efforts to link ecological, hydrologic, and geomorphic processes in a general theory of riverine dynamics, while further emphasizing the need to represent species biology and temporal change appropriately in such theory. Considering problems in lotic community ecology and conservation as the result of combinations of forces at multiple scales challenges us to extend our current conceptual models but holds considerable promise for improving our understanding and management of rivers and streams.

Acknowledgements

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