

Dendritic network structure constrains metacommunity properties in riverine ecosystems

B. L. Brown^{1*} and C. M. Swan^{2,3}

¹Department of Forestry & Natural Resources, Clemson University, Clemson, SC 29634, USA; ²Department of Geography & Environmental Systems; and ³Center for Urban Environmental Research & Education, University of Maryland, Baltimore County, Baltimore, MD 21250, USA

Summary

1. Increasingly, ecologists conceptualize local communities as connected to a regional species pool rather than as isolated entities. By this paradigm, community structure is determined through the relative strengths of dispersal-driven regional effects and local environmental factors. However, despite explicit incorporation of dispersal, metacommunity models and frameworks often fail to capture the realities of natural systems by not accounting for the configuration of space within which organisms disperse. This shortcoming may be of particular consequence in riverine networks which consist of linearly -arranged, hierarchical, branching habitat elements. Our goal was to understand how constraints of network connectivity in riverine systems change the relative importance of local vs. regional factors in structuring communities.

2. We hypothesized that communities in more isolated headwaters of riverine networks would be structured by local forces, while mainstem sections would be structured by both local and regional processes. We examined these hypotheses using a spatially explicit regional analysis of riverine macroinvertebrate communities, focusing on change in community similarity with distance between local communities [i.e., distance-decay relationships; (DDR)], and the change in environmental similarity with distance. Strong DDRs frequently indicate dispersal-driven dynamics.

3. There was no evidence of a DDR in headwater communities, supporting our hypothesis that dispersal is a weak structuring force. Furthermore, a positive relationship between community similarity and environmental similarity supported dynamics driven by local environmental factors (i.e., species sorting). In mainstem habitats, significant DDRs and community \times environment similarity relationships suggested both dispersal-driven and environmental constraints on local community structure (i.e., mass effects).

4. We used species traits to compare communities characterized by low vs. high dispersal taxa. In headwaters, neither strength nor mode (in-network vs. out of network) of dispersal changed our results. However, outcomes in mainstems changed substantially with both dispersal mode and strength, further supporting the hypothesis that regional forces drive community dynamics in mainstems.

5. Our findings demonstrate that the balance of local and regional effects changes depending on location within riverine network with local (environmental) factors dictating community structure in headwaters, and regional (dispersal driven) forces dominating in mainstems.

Key-words: dendritic networks, dispersal-driven community dynamics, distance-decay relationships, mass effects, metacommunity, species sorting

Introduction

Substantial variation in dispersal exists between organisms that contributes to the structuring of ecological communities

in space and time. While it would be naïve to suggest that community ecologists have been unaware of the influence of dispersal-driven processes on the structure and function of communities (McArthur and Wilson 1967), the magnitude of that influence has been marginalized. Only recently has community ecology really challenged the classic view of the

*Correspondence author. E-mail: bbrown3@clemson.edu

community as a localized and isolated entity and recognized the need to explicitly incorporate space and the movement of organisms into the theoretical and empirical investigations study of all communities rather than simply special cases (Holyoak, Leibold & Holt 2005). By conceiving local communities within a region as connected by a common regional species pool, the concept of the metacommunity addresses patterns and processes that may arise or vary across scales (Loreau 2000; Hubbell 2001; Shurin & Allen 2001). The concept recognizes two broad categories of effects – local and regional – and the potential interactions between local and regional effects (Urban 2004; Chase *et al.* 2005). Local effects are largely due to environmental constraints or species interactions, while regional effects are driven by the flux of organisms from the regional species pool (Amarasekare & Nisbet 2001; Chase *et al.* 2005).

This view of community assembly as a combination of local and regional influences has produced a recent flurry of creative research and important insights, but there are still some critical aspects of incorporating space into community ecology that are underappreciated. Connectivity between local communities has been widely appreciated (Kneitel & Miller 2003; Chase & Ryberg 2004), yet consideration of the actual configuration of local communities or dispersal networks has been limited. Recent theoretical work has investigated the effects of varying network structure on neutral metacommunities and found that spatial structuring changes γ -diversity (i.e., regional diversity) by altering α - and β -diversity across landscapes (Econo-mo & Keitt 2007). However, empirical examinations found that γ -diversity was unchanged by habitat geometry, despite considerable changes in α - and β -diversity (Starzomski & Srivastava 2007). Despite the obvious recognition that the spatial configuration of connections between communities can be an important determinant of community structure and even ecosystem functioning (France & Duffy 2006), there has been little research directly addressing this topic.

Much of the previous work on metacommunities has either not been explicit with regard to the spatial structuring of dispersal networks, or has focused on dispersal networks similar to those in Fig. 1a, b, in which dispersal is relatively equal among randomly - or uniformly -distributed patches on a landscape. Contrary to these previous conceptions of dispersal networks, the dispersal of many organisms is structured by dendritic habitat configurations as in Fig. 1c (Grant, Lowe & Fagan 2007). Dendritic networks have a hierarchical branching structure in which mainstems connect multiple blind-ended branches (Fig. 2). Moreover, in dendritic networks there are no 'patches'. Rather, the entire network represents potential habitat (Grant *et al.* 2007). On a landscape scale, the most obvious examples of dendritic networks are riverine systems.

Riverine systems are inherently dendritic in nature (Fagan 2002; Grant *et al.* 2007; Muneeppeerakul *et al.* 2008), consisting of headwater streams connected by larger mainstem channels. While these branching topologies distinguish riverine systems from most other ecological networks, it is the

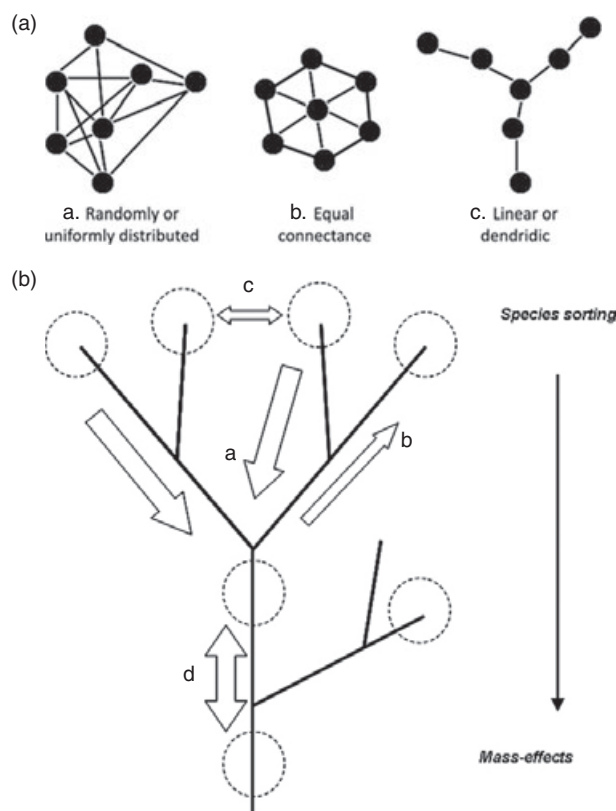


Fig. 1. (a) Example dispersal networks of metacommunities. Most theoretical and empirical investigations of metacommunities have explored systems with random, uniform, or equally -connected networks (a, b). However, many metacommunities may resemble panel (c) in which dispersal networks have linear or dendritic configurations. (b) Metacommunity dynamics that shape local communities change with position in a riverine network because of changes in dispersal. Thickness of white arrows corresponds to rate of dispersal. More organisms disperse from the headwaters to mainstems (a), and relatively few organisms are moving into headwaters (b). Exchange among localities in headwaters is low (c), but high in mainstems (d). Assuming that environmental conditions are at least somewhat important in determining species composition in both headwaters and mainstems, these differences in dispersal suggest that a species sorting model of metacommunities is most applicable for headwaters in dendritic networks, while mainstems should more resemble mass-effects metacommunities.

effect of these unique topologies on dispersal that may be most consequential for structuring riverine metacommunities. Because of their hierarchical structure, within-network flux of organisms in riverine networks is predicted to be greater through mainstems relative to headwaters because mainstems integrate movement of organisms from, and between, branches (Fagan 2002). This disparity in dispersal rate is exacerbated in riverine systems due to asymmetric movement of energy and matter from headwaters to mainstems. As a result of these disparities in dispersal, the forces that structure local communities in riverine systems may differ drastically in different sections of the drainage network. Assuming that the local environment exerts a similar influence throughout the riverine network, headwater communities would primarily be structured by local factors while

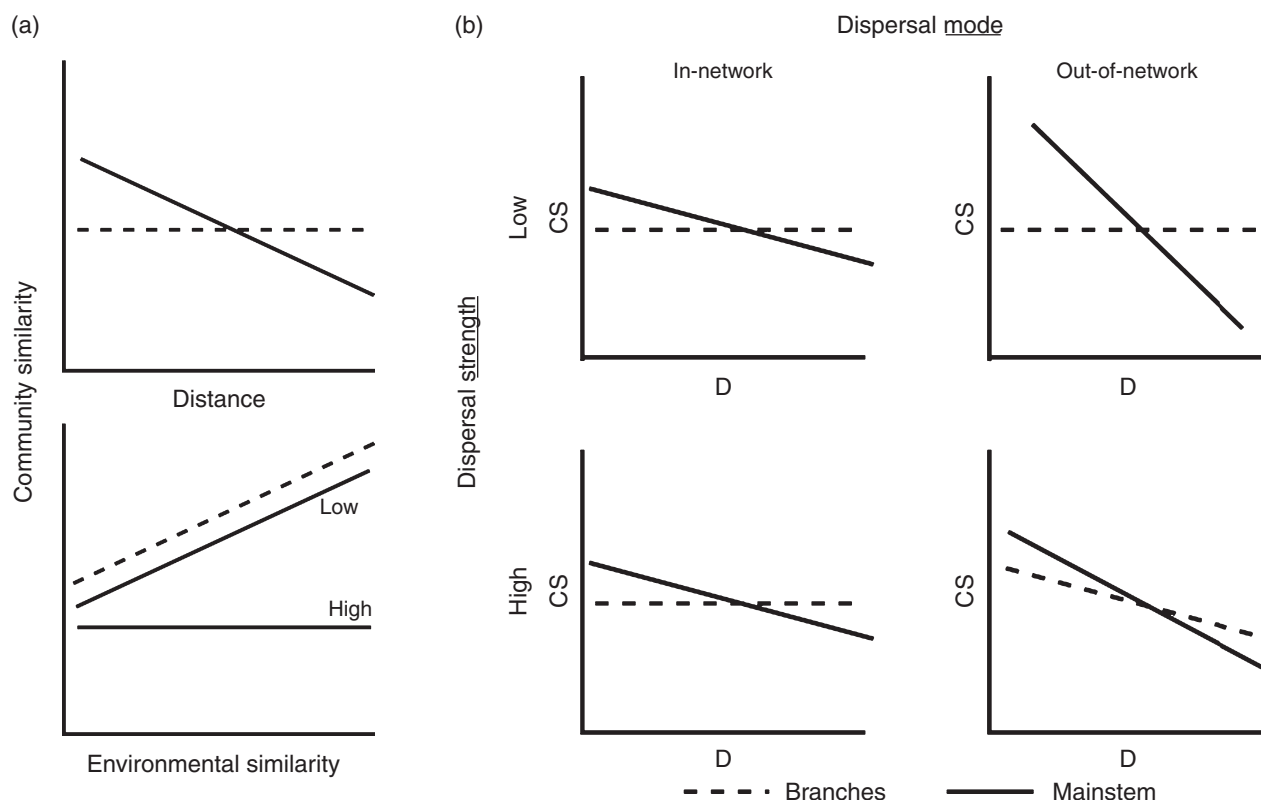


Fig. 2. (a) Predicted metacommunity patterns in species sorting (dotted lines) and mass effects (solid lines) metacommunities. 'low' and 'high' refer to the average propensity for dispersal within communities. (b) Distance-decay relationships for dendritic metacommunities based on dispersal strength (High vs. Low) and dispersal mode (within network vs. out of network).

mainstem communities are expected to be structured by a combination of local and regional (i.e., dispersal) factors (Fig. 2). These two scenarios correspond to two different conceptual paradigms of metacommunities: *species sorting* and *mass effects* (Chase *et al.* 2005). In *species sorting* metacommunities, local community structure is controlled by the 'sorting' of species into their most appropriate habitat based on classic niche principles and are thus primarily driven by local factors (Chase *et al.* 2005). In *mass effects* metacommunities, the local environment still exerts an influence on community structure, but high rates of dispersal can swamp or interact with local influences so that local community structure is largely driven by regional processes (Amarasekare 2004; Chase *et al.* 2005). It is therefore possible that both types of metacommunities may be found within the same drainage network due to the influence of network structure on dispersal of organisms.

However, we would not predict that differences in community structure in different sections of riverine networks would be solely the product of differences in dispersal. Headwater streams are unique habitats, varying substantially in temperature, flow regime, and gradient within and across physiographic provinces (Meyer *et al.* 2007; Clarke *et al.* 2008). They provide refugia from predation to competition, as well as serve as spawning habitat and prime foraging areas (Meyer *et al.* 2007; Matthews & Robison 2009;). In addition to being the most isolated habitats in riverine networks, the multivari-

ate suite of abiotic factors in headwaters differs substantially from downstream habitats (Benda *et al.* 2004) so that mainstems likely serve as strong environmental filters on migration between headwater sites (Creed 2006; Meyer *et al.* 2007). This is not to suggest that mainstem communities are not subject to environmental filtering (e.g., flow regime; Poff & Ward 1995), but in headwaters, strong environmental filtering coupled with isolation from the regional species pool suggest that the main structuring mechanisms in headwater metacommunities should be local. Furthermore, there is some evidence that environmental conditions in headwater streams do not vary predictably across space in riverine networks (Clarke *et al.* 2008). Thus, as predicted by general metacommunity theory and applied to riverine networks, metacommunities of higher order streams (i.e., mainstems) should be structured according to a mass-effects paradigm of metacommunity structure due to the likely strong influence of dispersal on community structure swamping the effects of species interactions and environmental filtering on community structure (Kunin 1998). Headwater stream metacommunities should follow a species sorting paradigm since local environmental conditions and species interactions should be the driving force behind community structure.

One useful methodology for detecting the influence of dispersal on community structure is the analysis of distance-decay relationships (DDRs), illustrated conceptually in the top panel of Fig. 2a (also see Nekola & White

1999; Soininen, Lennon & Hillebrand 2007a for background on DDR methods and application). DDRs relate the pairwise similarity of local communities to the distance between those communities and have been investigated in a large number of natural systems (Soininen, McDonald & Hillebrand 2007b). DDRs have also been used to structure predictions regarding empirical patterns that should emerge under different metacommunity paradigms with negative DDRs generally considered to be indicative of dispersal-driven dynamics (Nekola & White 1999; Chase *et al.* 2005). However, for DDRs to be truly informative regarding the relative influences of local and regional effects on metacommunities, their interpretation is necessarily accompanied by an investigation of the change in environmental conditions across the same spatial gradient since environmental conditions are also expected to change across space (Nekola & White 1999; Chase *et al.* 2005). Fig. 2a illustrates predicted DDRs and community similarity \times environmental similarity relationships expected under species sorting and mass effects metacommunities.

A second consideration when using DDRs to investigate metacommunity dynamics is the measure of distance employed in constructing the similarity \times distance and environment \times distance relationships. While simple Euclidean distance is appropriate in many cases, other measures of distance might be appropriate or informative depending on the topology of the dispersal network. The way in which distance is defined may be especially consequential for dendritic networks like riverine systems in which dispersal of many organisms follows the branching network structure (i.e., network distance) rather than simple straight lines between local communities (Fig. 1b; Grant *et al.* 2007). In such cases, distance defined along network pathways might more realistically represent the dispersal of organisms as opposed to shortest distance (i.e., Euclidean distance) between local communities (Fagan 2002; Grant *et al.* 2007; Muneerpeerakul *et al.* 2008; Grant, Green & Lowe 2009). In addition, some organisms are not confined to dispersal within the network, and this out-of-network dispersal (OND) may play a major role in metapopulation or metacommunity dynamics (Grant *et al.* 2007, 2009). The importance of OND has been predicted by theory (Fagan 2002; Grant *et al.* 2007) and demonstrated empirically for several taxa including salamanders (Grant *et al.* 2009) and the adult phase of aquatic insects (Macneale, Peckarsky & Likens 2005). For some organisms, dispersal mode – and thus the best descriptor of dispersal distance – changes with age or life-stage (Macneale *et al.* 2005; Grant *et al.* 2009).

In this study we examined metacommunity structure in a riverine network using a large, publicly-available data set on macroinvertebrate communities (Maryland Department of Natural Resources 1993). Our analysis had two primary goals. First, we used basic spatial ecological patterns, i.e., DDRs and related patterns, to infer the relative influence of local vs. regional processes in structuring macroinvertebrate metacommunities across three Maryland (USA) watersheds. Second, we examined whether our conclusions about the rel-

ative influence of local and regional processes in structuring riverine metacommunities were dependent on location of local communities within the network, i.e., whether processes differed from headwaters to mainstems. To inform our analyses and generate predictions regarding the role of dispersal in structuring riverine metacommunities, we also utilized published data on dispersal-related traits of macroinvertebrate species (Poff 1997). We made the following predictions based on metacommunity theory and general knowledge of riverine systems:

1. Metacommunity structure

- (i) A species-sorting paradigm would best describe headwaters metacommunities and therefore we would find: (1) no significant DDRs; (2) no strong relationships between environmental similarity and distance; (3) strong positive correlation between community similarity and environmental similarity (Fig. 2a).
- (ii) A mass effects paradigm would best describe mainstem metacommunities and we would therefore predict: (1) strong DDRs indicating dispersal-driven dynamics, (2) a moderate to strong relationship between environmental similarity and distance; (3) probable positive correlation between community similarity and environmental similarity. The strength of (2) and (3) will depend on the strength of dispersal (Fig. 2a).

2. Role of dispersal

- (i) In headwater communities, increasing either the strength or mode (within-network vs. OND) of dispersal will have little effect on DDRs since community composition is primarily dictated by local conditions (Fig. 2b).
- (ii) In mainstem communities, increasing dispersal strength will weaken DDRs, particularly when there is a high level of OND (Fig. 2b). This weakening occurs due to relaxation of dispersal limitation within the same spatial scale.

We tested the first set of predictions by examining DDRs and related spatial relationships. The second set of predictions were tested by using traits to examine how DDRs and related spatial patterns differed between communities characterized by high and low dispersal ability/propensity.

Materials and methods

We used data from the Maryland Biological Stream Survey (MBSS) to investigate metacommunity properties of three riverine networks. The MBSS data set contains data on community structure for benthic macroinvertebrates and habitat measurements collected by the Maryland Department of Natural Resources (MDDNR) (1993). Sampling is described extensively elsewhere (MDDNR, <http://www.dnr.state.md.us/streams/mbss/>). Environmental variables included water chemistry (pH, dissolved organic carbon, nitrate, sulfate), dissolved oxygen, temperature, conductivity, hydrologic parameters (maximum depth, gradient, average width, average thalweg width, average velocity, discharge, percent embeddedness), riparian width, and watershed landuse (percent urban, agricultural, coniferous, deciduous, mixed forest). For the biota, a 75 m reach was delineated and sampling of invertebrates involved taking $n = 20$,

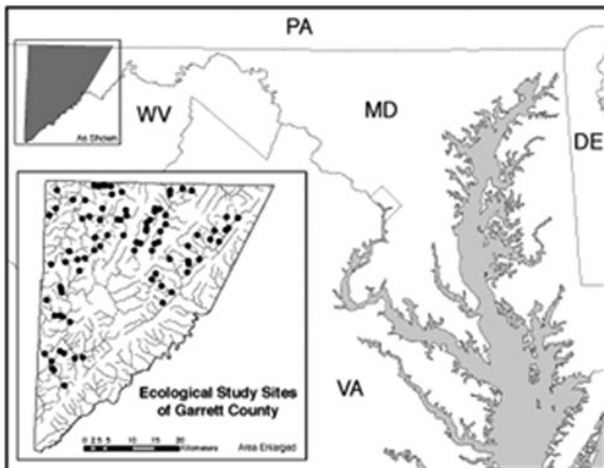


Fig. 3. We used 91 sites from the Maryland Biological Stream Survey (MBSS) from Garrett County, MD, USA in our investigation of metacommunity structure in stream networks.

0.10 m² samples with a 500 µm D-net in proportion to the dominant habitat features in the reach. Samples were preserved in 70% ethanol, and sub-samples taken that comprised > 100 individuals identified to genus. Invertebrates were sampled in the spring (March–April; 1999–2001). We focus our investigation on 91 relatively undisturbed sites (> 25% forested watershed landuse) in three drainages (Youghiogheny, Savage, Casselman Rivers; Fig. 3) located on the Appalachian Plateau in Garrett County, MD, USA.

We concentrated on the relationships between three sets of variables: distance between sites, community similarity between sites, and environmental similarity between sites. The relationship between community similarity and distance is commonly referred to as the distance-decay relationship (DDR) and has been the subject of considerable study in ecology and biogeography (Nekola & White 1999; Soininen *et al.* 2007b); DDRs form the centerpiece of our investigation. Distance between sites was considered to be an independent variable, measured with relatively little error and thus an appropriate predictor for regression analysis. We calculated distance between sites in two ways. (1) Euclidean distance = the shortest distance between sites in two-dimensional space. (2) Network distance = the distance between sites following the dispersal pathways dictated by the riverine dendritic network.

Using ArcGIS (version 9.2), we calculated both Euclidean (Hawth's Analysis Tool Plug in V 3.27) and network distance (i.e., distance between sites along the river network; Network Analysis Toolbox/OD Cost Matrix Analysis Tool) between all sites within each drainage. We used the Bray-Curtis index of similarity to quantify the degree of community similarity between sites. The Bray-Curtis index is commonly utilized in characterizing ecological communities and has been recommended for study of DDRs (Morlon *et al.* 2008). We used untransformed proportional species abundances since our goal was to evaluate actual similarity between communities rather than emphasizing the role of rare species. However, we also examined patterns using Jaccard's index (an incidence-based index) and found that relationships were qualitatively unchanged in all analyses where we report Bray-Curtis similarities.

Our index of environmental similarity was based on a multivariate representation of aquatic habitat variables measured in the MBSS data set. There are 61 measured habitat parameters included in the MBSS data set. However, we limited the number of variables

included in our index to 21 (listed above) for a number of reasons. Many variables in the original data set were highly redundant and we used only a single representative from sets of redundant variables. For example, we chose to use pH measured in the field and to omit pH measured in the laboratory. We also excluded indices (e.g., the Hilsenhoff biotic index), as well as several variables in the larger MBSS data set that were not applicable to our region of interest, for example, extent of local coal-mining activity. The variables retained in our analysis were primarily basic measures of water chemistry, channel flow status, and local land-use conditions. We ordinated data on the 91 MBSS sites using principal components analysis (PCA) with a secondary correlation matrix. From this PCA, we retained all of the principal components with eigenvalues greater than one and our measure of environmental similarity was the distance between pairs of sites measured using Euclidean distance in multivariate space. We also used multi-response permutation procedure (MRPP) performed on the PCA scores to test the hypothesis that headwaters and mainstems were distinct in terms of environmental variables. In addition, the variability among sites was compared for headwaters and mainstems by calculating the average distance to the centroid of each group in PC space.

While environmental gradients were identified using the multivariate analysis described above for all 91 sites of regional interest, we used least squares regression to examine three sets of relationships within headwaters and mainstem reaches separately. We defined headwaters as first order streams, and mainstems as third order streams, which were the most downstream sites in the MBSS data set. Headwaters ($n = 22$) were shallow (maximum average depth, 38 cm, range 14–114 cm), narrow (average wetted width, 2.4 m, range 0.4–4.3 m) and relatively slow flowing (average baseflow velocity 0.10 m s⁻¹, range 0.01–0.23 m s⁻¹). Mainstem sites ($n = 30$) had an average maximum depth of 62 cm (range, 24–112), average wetted width of 9.1 m (range, 3.6–17.2), and average baseflow velocity of 0.18 m s⁻¹ (range, 0.05–0.66 m s⁻¹). DDRs, the relationship between environmental similarity and distance between sites, and the relationship between community similarity and environmental similarity were calculated for headwaters and mainstems separately. As pairwise data are inherently non-independent, all regression statistics were generated using permutation tests (Manly 1991) with 1000 random permutations. One potential criticism of our approach is that the use of Mantel tests are the standard method for separating local (i.e., environmental) from regional (i.e., distance) effects on community similarity and thus metacommunity structure (Borcard, Legendre & Drapeau 1992). However, because we are pooling sites from multiple watersheds and did not calculate similarities across watershed boundaries, our data produce an incomplete matrix (i.e., values do not exist for every matrix cell) precluding the use of Mantel tests.

In order to examine the influence of species traits on metacommunity patterns, we chose five traits describing dispersal ability of the taxa found at our sites and used the values of these traits to divide the 52 communities in our data set into 'high' and 'low' dispersal communities. Two traits were associated with adult dispersal (female dispersal distance, flying strength) and three associated with within-channel larval dispersal (drift propensity, swimming strength, crawling strength). Binary trait values were matched from a published data-base (Poff *et al.*, 2006) and we calculated the average trait score for each local community as $\sum_{i=1}^n ty_i/n$ where t is the binary trait value (0 or 1), y is abundance of species i , and n is the number of species in the local community. We assigned local communities to high or low dispersal communities based on whether average trait value was

above or below the median for the 52 MBSS sites, then re-calculated DDRs separately for low and high dispersal communities. We followed this procedure for each of the five dispersal-related traits. In addition, for traits with the potential to reveal OND, we calculated DDRs using both network distance (i.e., distance within the riverine network) and Euclidean distance which would be expected to more closely approximate overland flight. We estimated the significance and strength of each DDR using permutation tests as previously described.

Results

The PCA upon which we based our measure of environmental similarity identified three gradients related to hydrology, land-use and water chemistry. In our calculation of environmental similarity, we used seven principal components (PC) which explained 71% of the variance in the 21-variable data set. The first three principal components alone explained 46% of the variability and were clearly defined by distinct groups of variables. The first component (PC1) explained 20% of variance and was strongly related to hydrologic parameters, most notably average thalweg depth ($r = 0.83$), average stream width ($r = 0.81$), and mean flow ($r = 0.76$). PC2 explained 15% of total variance and was highly correlated with land-use variables including % agricultural development ($r = 0.83$) and % deciduous forest cover ($r = -0.66$). PC3 explained 11% variability and was strongly correlated with stream dissolved oxygen ($r = -0.72$) and water temperature ($r = 0.58$). Headwaters and mainstems were distinct with regard to environmental characteristics (Fig. 4). The differences between sites were most identifiable most along principal component one which represented a hydro-

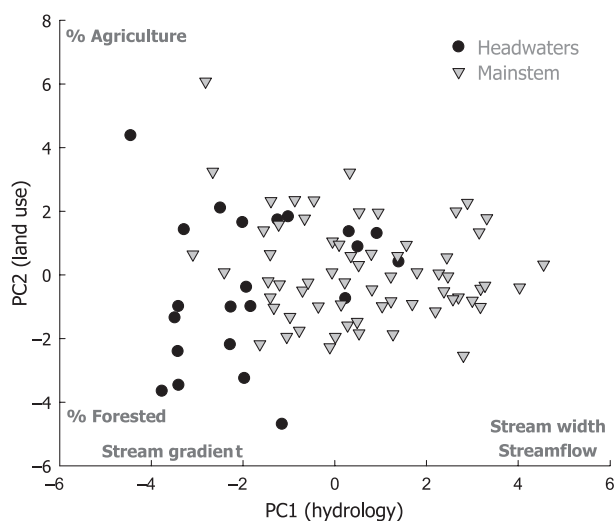


Fig. 4. First two axes of a principal components analysis based on environmental variables in the MBSS data set. Labels immediate inside the axes indicate variables that were strongly correlated with each axis. The first axis was primarily composed of hydrologic variables while the second was primarily representative of land-use. Headwaters and mainstems differed significantly based on the ordination (MRPP, $P(\Delta) = 0.0002$).

logy gradient but there was also a trend towards headwaters being more forested (principal component 2). A test of differences between headwaters and mainstems was highly significant on these two axes (multi-response permutation procedure; $P(\Delta) = 0.0002$). Average distance to the centroid, i.e., variability among sites, was headwaters = 2.90 ± 0.26 (mean \pm 1SE); mainstems = 3.53 ± 0.18 .

A core component of our analysis was an examination of the distance-decay of community similarity between sites for headwater and mainstem areas. For headwater sites, we found no evidence of any significant DDR (Fig. 5a). However, between mainstem sites, there was a significant and relatively strong DDR (Fig. 5b). This combination of patterns suggests that dispersal-driven dynamics were important in explaining community structure in mainstem sites, but not headwater locations.

We measured differential spatial dependence of environmental factors between headwaters and mainstems (Fig. 5c,d). Environmental similarity generally decreased with increasing distance across all 52 headwater and mainstem sites, although the relationship was only significant at mainstem sites (Fig. 5c,d). Furthermore, r^2 was $8.2 \times$ higher in mainstem sites compared with branches (Fig. 5c,d). However, there were significant, positive relationships between community similarity and environmental similarity for both headwaters (Fig. 5e) and mainstem sites (Fig. 5f) with a stronger relationship observed (i.e., higher slope and r^2) for mainstem sites than headwaters.

There were several noteworthy differences in DDRs between communities characterized as 'high' and 'low' dispersal, as well as differences in results from headwaters to mainstems (Table 1). Most striking was that headwater sites never produced significant DDRs even when parsed into high and low dispersal groups. For traits describing only within-network dispersal potential (drifting, swimming, crawling), dispersal limitation was only evident at mainstem sites for two of the three traits for strong dispersers (Table 1). In addition, for those traits related to potential OND (i.e., female dispersal ability, adult flying strength), we observed significant DDRs for poorly dispersing communities only among mainstem locations, but never for headwater sites (Table 1). This was true regardless of how we analyzed connectivity between sites – as Euclidean distance between sites or as distance along the network. For communities characterized by strong dispersers, we found significant DDRs in mainstems for one trait (female dispersal ability), and only when analyzed as a function of network distance (Table 2).

Discussion

Our goals in this study were to evaluate the relative strength of local vs. regional processes in dictating metacommunity structure in riverine systems. Based on metacommunity theory and general knowledge of riverine systems, we made predictions about the mechanisms that structure riverine metacommunities and the empirical patterns that should

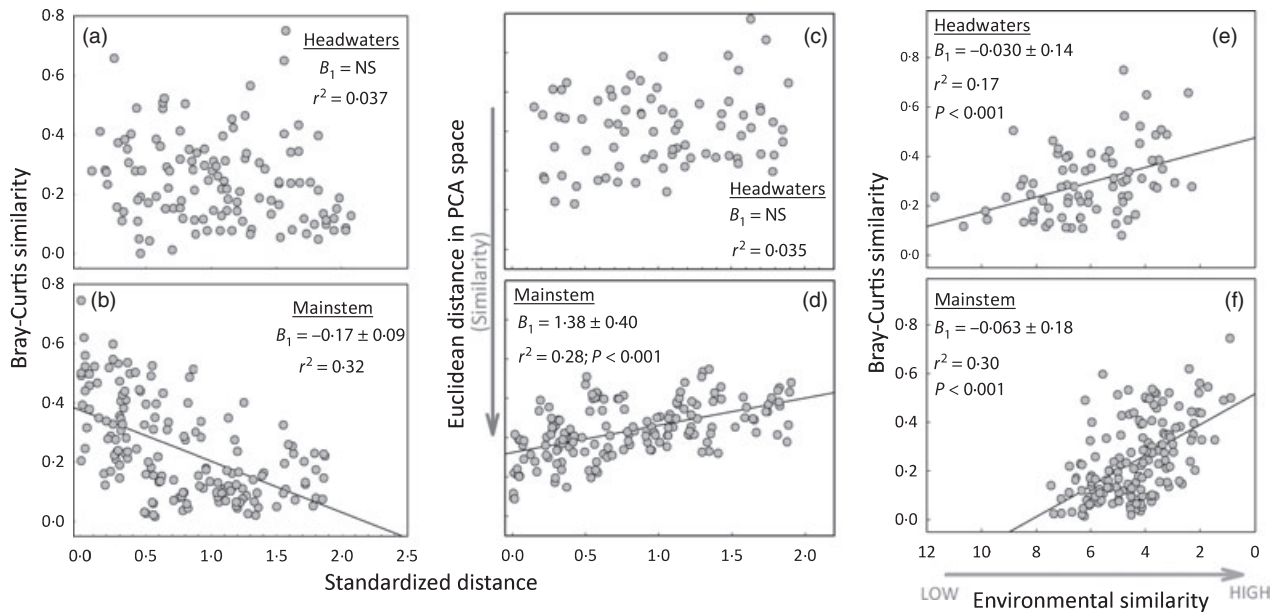


Fig. 5. Relationships between community similarity and environmental similarity across differences within watersheds in the MBSS data set. **a & b:** Distance-decay relationships for benthic macroinvertebrates across the 52 MBSS sites in headwaters (a) and mainstems (b). **c & d:** Relationship between distance and environmental similarity at the 52 MBSS site in headwaters (c) and mainstems (d). Our metric of environmental similarity measured variance and is therefore inversely-related to similarity, i.e., large values of the index indicate low similarity. **e & f:** Correlation between community similarity and environmental similarity for the 52 MBSS sites in headwaters (e) and mainstems (f).

Table 1. 95% confidence intervals and coefficients of determination for (a) distance-decay relationships, (b) environmental similarity \times distance relationships, and (c) community \times environmental similarity for benthic macroinvertebrate communities at 52 stream sites in Garrett County, MD (Fig. 3). Slopes are least squares fits. Confidence intervals and coefficients of determination are based on permutation tests (1000 randomizations)

Relationship	Location	Slope	Upper 95%	Lower 95%	r^2
Distance-decay	Branches	0 (NS)	—	—	0.037
	Mainstems	-0.16	-0.115	-0.205	0.32
Environment \times distance	Branches	0 (NS)	—	—	0.034
	Mainstems	0.21	0.27	0.15	0.28
Environment \times community	Branches	-0.030	-0.015	-0.045	0.17
	Mainstems	-0.063	-0.042	-0.082	0.30

'NS' = no significant slope

emerge as a result. We predicted that metacommunities in headwaters would be structured according to a species sorting paradigm, while mainstems would be structured according to a mass effects paradigm. We also predicted that increased dispersal strength based on species traits within the community should weaken DDRs in mainstems due to relaxation of dispersal limitation, while DDRs of headwaters would remain unchanged. Both sets of predictions were strongly supported by our results, and our major finding was that the balance of local and regional forces in shaping local communities changes appreciably depending on position within a riverine network. In fact, a comparison of headwa-

ters and mainstems reveals two distinctly different metacommunity paradigms.

As predicted, metacommunity patterns in headwaters were consistent with the species sorting paradigm. The lack of a significant DDR in headwaters was one indication of dynamics not driven by dispersal (Fig. 5a). However, the significant positive relationship between community similarity and environmental similarity (Fig. 5e) coupled with the lack of relationship between environmental similarity and distance between sites (Fig. 5c) was even more revealing. However, headwater community similarity was still significantly related to environmental similarity. Taken together, these three patterns seem to indicate that community composition in headwaters is dictated by local environmental factors, but that neither community similarity nor environmental similarity change predictably with distance, i.e., community structure is not dispersal-driven. These results are consistent with empirical patterns predicted under a species sorting metacommunity paradigm (Fig. 2a). In contrast, our analysis of mainstems produced results consistent with a mass effects metacommunity. There was a relatively strong DDR (Fig. 5b), as well as strong community similarity \times environmental similarity (Fig. 5f) and environmental similarity \times distance (Fig. 5d) relationships. This combination of patterns suggests that both environmental filtering and dispersal driven processes dictate community structure in mainstem metacommunities, consistent with predictions based on mass effects (Fig. 2a). These results contrast to previous work that found no predictable influence of environmental factors on community similarity in mainstems (Lloyd, Nally & Lake 2005). However, the study did not evaluate the potential role of dispersal.

Table 2. Incorporating species traits into our regional analysis

Trait	Location	Low dispersal	High dispersal
Female dispersal (<i>Euclidean</i>)	Branches	NS	NS
	Mainstem	$-0.054 \pm 0.04; 0.094$	NS
Female dispersal (<i>Network</i>)	Branches	NS	NS
	Mainstem	$-0.14 \pm 0.08; 0.28$	$-0.17 \pm 0.09; 0.30$
Adult flight (<i>Euclidean</i>)	Branches	NS	NS
	Mainstem	$-0.12 \pm 0.08; 0.12$	NS
Adult flight (<i>Network</i>)	Branches	NS	NS
	Mainstem	$-0.13 \pm 0.05; 0.28$	NS
Drifting propensity	Branches	NS	NS
	Mainstem	$-0.10 \pm 0.06; 0.18$	$-0.11 \pm 0.06; 0.21$
Swimming strength	Branches	NS	NS
	Mainstem	$-0.18 \pm 0.08; 0.32$	$-0.12 \pm 0.11; 0.18$
Crawling strength	Branches	NS	NS
	Mainstem	$-0.17 \pm 0.07; 0.33$	NS

Statistics give slope ($\pm 95\%$ CI) and r^2 of least squares fits produced through permutation tests. NS = no significant slope. For the traits female dispersal and adult flight, we calculated DDRs using distance between sites defined two ways – along the dendritic network and as Euclidean distance – since both traits describe potential OND that can occur overland.

One important caveat is that, with our regression-based analysis, it is difficult to separate the effects of dispersal limitation from the influence of environment since both change across the same spatial gradient. However, our use of species traits addresses this issue and complements our spatial analysis.

Our use of species traits was revealing for two reasons. First it helped to clarify potential mechanisms suggested by our spatial analysis of community structure. A species sorting paradigm predicts that DDRs should not change regardless of dispersal rates. However, lack of dispersal driven dynamics is not the only mechanism that can produce a null DDR. A null DDR may also be the result of ubiquitous dispersal, i.e., everything disperses everywhere. However, if the 'everything gets everywhere' mechanism were responsible for the null DDR, then we would predict that there might be detectable DDRs for communities characterized by low dispersal when compared with high dispersal communities (Fig. 2b). We did not see any such differences in our headwater communities for any of the 5 dispersal traits (Table 1), suggesting that the null relationship in headwater communities was the result of a lack of dispersal-driven processes rather than the result of ubiquitous dispersal. However, the same analysis across mainstem sites did show differences between high and low dispersal communities (Table 2). There were qualitative differences in three of the five dispersal-linked traits we examined (Table 1) and, furthermore, for these three traits there were significant DDRs for low-dispersal communities and no significant DDRs in high dispersal communities (Table 1). These results provide evidence that dispersal limitation is driving the DDR (Fig. 5b), and that both dispersal limitation and environmental sorting are influencing mainstem meta-communities. Interestingly, while some existing evidence suggests that environmental conditions in headwater streams change less predictably across space than do mainstem sites (Clarke *et al.* 2008), our analysis did not conform to this expectation. Rather, we found that while headwaters and

mainstems were distinct with regard to environmental characteristics at our disposal, mainstem habitats were actually slightly more variable among sites, a finding that is congruous with the result that local environmental conditions were important in determining community composition in both headwaters and mainstems.

Our use of traits also highlighted the potential importance of OND for benthic macroinvertebrate communities. Two of the traits we utilized, female dispersal and overland flight strength, combine dispersal pathways, i.e., they may be described as both within-network and OND. This is true because flight ability of the adult phase of benthic macroinvertebrates allows these organisms to disperse overland between streams or even watersheds (Macneale *et al.* 2005; Finn & Poff 2008). The overland distances that adult benthic macroinvertebrates can span varies considerably with both species and environmental condition (Briers, Cariss & Gee 2003; Finn & Poff 2008) and differences in adult dispersal differences are measurably related to population genetic structure (Miller, Blinn & Keim 2002). Using isotopic markers, individuals have been documented to travel as far as 500 m overland (Macneale *et al.* 2005), but adult dispersal is relatively understudied for aquatic insects (Petersen *et al.* 2004) and possible dispersal distances are likely even higher. For the two traits that potentially represent OND, we calculated DDRs using both network distance and Euclidean distance, with the Euclidean distance predicted to be a better descriptor of overland dispersal. Of these two traits, one (female dispersal) produced significant DDRs for both high and low dispersal communities with the network distance, but only produced a significant DDR for low dispersal communities with Euclidean distance, suggesting that female dispersal may be influencing community similarity via OND (Table 1). For the adult flight trait, there were significant DDRs for low dispersal communities, but not for high dispersal communities (Table 1). This was true with both the Euclidean and network distances, suggesting that adult flight may be influ-

encing community similarity through both within-network and OND. Such a result would be consistent with the knowledge that, while adults do travel overland for significant distances, their flight tends to be biased upstream and concentrated along riverine corridors (Petersen *et al.* 1999, 2004; Macneale *et al.* 2005).

We propose three, not necessarily exclusive, interpretations of why both dispersal limitation and environmental filtering was found to occur simultaneously in mainstem sites. First, in riverine ecosystems, downstream localities should receive a higher rate of recruitment and therefore display community structure dictated, in large part, by regional processes. Local conditions may also be important, but high rates of dispersal from other sections of the network and the regional species pool drive random divergence between local communities so that those further apart tend to diverge in species composition more markedly (Cottenie & de Meester 2003; Chase *et al.* 2005). Second, the high rate of movement due to disturbance (i.e., catastrophic drift) could drive the dispersal limitation signal, despite strong influence of local effects on community structure (Townsend 1989). In the extreme case, disturbance might completely erase any local signal (Townsend 1989). Finally, there is substantial evidence that interspecific variation in dispersal ability likely blurs the distinction between neutral processes and species-sorting. Thompson & Townsend (2006) identify many instances where both environmental factors and distance explain variation in community similarity in New Zealand streams. Together, these interpretations suggest the patch-dynamic concept as a plausible third explanation for the patterns we identify here. High rates of dispersal between and among taxa, coupled with a strong disturbance gradient have been repeatedly found to be major factors in understanding community assembly in streams (Townsend 1989).

Despite clear results, one major limitation inherent in our study is that our work is based on macroinvertebrate samples taken on single dates in March and April at each of the 52 sampling locations. Thus, the data provide only a snapshot in time. Riverine macroinvertebrate communities are notoriously dynamic due to high species diversity, fairly rapid life cycles, and life histories that span multiple habitats within a single year. It is certainly possible that there are strong seasonal shifts in the factors that shape riverine metacommunities. In Maryland, USA, environmental conditions fluctuate fairly dramatically throughout the year and aerial dispersal of macroinvertebrates is strongly seasonal. Changes in either local environmental filters or in dispersal dynamics could certainly alter the factors shaping the metacommunity. Thus, different paradigms of metacommunity structure may exist not only spatially, but also temporally within riverine networks. We therefore suggest that adding a temporal component to analyses of DDRs might provide an informative and fruitful avenue for research.

Our investigation revealed different metacommunity patterns occurring simultaneously within watersheds. As such, there are interesting basic and applied implications for the types of communities we see and the ecological/evolutionary

factors structuring them. As topographic low-points in the landscape, streams and rivers accumulate the effects of both natural and anthropogenic disturbances occurring in terrestrial ecosystems. Efforts to harness hydrologic variability manifest as complex, spatially-disrupted patterns in riverine network structure, often leading to wholesale loss of headwater streams (Bernhardt & Palmer 2007). Such disruption might alter the advective forces shaping the metacommunity processes at work in downstream environments explaining, in part, how local communities are structured in more highly disturbed reaches. Subsequent alterations in species composition and, perhaps, richness might then have implications for important ecosystem processes, such as nutrient cycling by primary consumers (e.g. Poff, Wellnitz & Monroe 2003). Understanding the spatial context for habitats within riverine networks might be pivotal to restorationists interested in the re-establishment of 'natural' communities in restored areas. Thus, another fruitful area of research would be to investigate how the patterns we revealed here compare across land-use gradients and in restored ecosystems.

Acknowledgements

We would like to thank Joe School for his assistance with the MBSS site map and Chris Fricke for his assistance with calculations of distance between sites. Rob Baldwin, Robert Creed, Winsor Lowe, and Mathew Leibold all provided conversation and criticism that refined our thinking on metacommunities and dendritic networks. We especially appreciate all of the hard work by the Maryland Department of Natural Resources in collecting the data comprising the MBBS data set. We would also like to thank two anonymous reviewers who provided valuable critiques of our work.

References

- Amarasekare, P. (2004) Spatial variation and density-dependent dispersal in competitive coexistence. *Proceedings of the Royal Society of London B*, **271**, 1497–1506.
- Amarasekare, P. & Nisbet, R.M. (2001) Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *The American Naturalist*, **158**, 572–584.
- Benda, L.E., Poff, N.L., Miller, D., Dunne, T., Reeves, G.H., Pess, G. & Pollock, M. (2004) The Network Dynamics Hypothesis: How channel networks structure riverine habitats. *BioScience*, **54**, 413–427.
- Bernhardt, E. & Palmer, M.A. (2007) Restoring streams in an urbanizing world. *Freshwater Biology*, **52**, 738–751.
- Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.
- Briers, R.A., Cariss, H.M. & Gee, J.H.R. (2003) Flight activity of adult stoneflies in relation to weather. *Ecological Entomology*, **28**, 31–40.
- Chase, J.M. & Ryberg, W.A. (2004) Connectivity, scale-dependence, and the productivity-diversity relationship. *Ecology Letters*, **7**, 676–683.
- Chase, J.M., Amarasekare, P., Cottenie, K., Gonzalez, A., Holt, R.D., Holyoak, M., Hoopes, M.F., Leibold, M.A., Loreau, M., Mouquet, N., Shurin, J.B. & Tilman, D. (2005) Competing theories for competitive metacommunities. *Metacommunities: Spatial Dynamics and Ecological Communities* (eds M. Holyoak, M.A. Leibold & R.D. Holt). pp. 335–354, University of Chicago Press, Chicago and London.
- Clarke, A., MacNally, R., Bond, N.R. & Lake, P.S. (2008) Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology*, **53**, 1707–1721.
- Cottenie, K. & de Meester, L. (2003) Connectivity and cladoceran species richness in a metacommunity of shallow lakes. *Freshwater Biology*, **48**, 823–832.
- Creed, R.P. (2006) Predator transitions in stream communities: a model and evidence from field studies. *Journal of the North American Benthological Society*, **25**, 533–544.
- Economo, E.P. & Keitt, T.H. (2007) Species diversity in neutral metacommunities: a network approach. *Ecology Letters*, **10**, 1–11.

- Fagan, W.F. (2002) Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, **83**, 3243–3249.
- Finn, D.S. & Poff, N.L. (2008) Emergence and flight activity of alpine stream insects in 2 years with contrasting winter snowpack. *Arctic, Antarctic, and Alpine Research*, **40**, 638–646.
- France, K.E. & Duffy, J.E. (2006) Diversity and dispersal interactively affect predictability of ecosystem function. *Nature*, **441**, 1139–1143.
- Grant, E.H.C., Lowe, W.H. & Fagan, W.F. (2007) Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters*, **10**, 165–175.
- Grant, E.H.C., Green, L.E. & Lowe, W.H. (2009) Salamander occupancy in headwater stream networks. *Freshwater Biology*, **54**, 1370–1378.
- Holyoak, M., Leibold, M.A. & Holt, R.D. (2005) *Metacommunities: Spatial Dynamics and Ecological Communities*, pp. 513. University of Chicago Press, Chicago and London.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Kneitel, J.M. & Miller, T.E. (2003) Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *American Naturalist*, **162**, 165–171.
- Kunin, W.E. (1998) Biodiversity at the edge: a test of the importance of spatial 'mass effects' in the Rothamsted Park Grass experiment. *Proceedings of the National Academy of Sciences, USA*, **95**, 207–212.
- Lloyd, N.J., Nally, R.M. & Lake, P.S. (2005) Spatial autocorrelation of assemblages of benthic invertebrates and its relationship to environmental factors in two upland rivers in southeastern Australia. *Diversity & Distributions*, **11**, 375–386.
- Loreau, M. (2000) Are communities saturated? On the relationship between alpha, beta, and gamma diversity. *Ecology Letters*, **3**, 73–76.
- Macneale, K.H., Peckarsky, B.L. & Likens, G.E. (2005) Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors. *Freshwater Biology*, **50**, 1117–1130.
- Manly, B.F.J. (1991) Chapter 8: regression analysis. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, pp. 148–171. CRC Press, London.
- Maryland Department of Natural Resources (MDDNR). Maryland Biological Stream Survey. Maryland Department of Natural Resources Assessment Service Monitoring and Non-Tidal Assessment Division. <http://www.dnr.state.md.us/streams/mbss/>.
- Matthews, W.J. & Robison, H.W. (2009) Influence of drainage connectivity, drainage area and regional species richness on fishes of the interior highlands in Arkansas. *The American Midland Naturalist*, **139**, 1–19.
- Meyer, J.L., Strayer, D.L., Wallace, J.B., Eggert, S.L., Helfman, G.S. & Leonard, N.E. (2007) The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association*, **43**, 86–103.
- Miller, M.P., Blinn, D.W. & Keim, P. (2002) Correlations between observed dispersal capabilities and patterns of genetic differentiation in populations of four aquatic insect species from the Arizona White Mountains, U.S.A. *Freshwater Biology*, **47**, 1660–1673.
- Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. & Green, J.L. (2008) A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters*, **11**, 904–917.
- Muneepeerakul, R., Bertuzzo, E., Lynch, H.J., Fagan, W.F., Rinaldo, A. & Rodriguez-Iturbe, I. (2008) Neutral metacommunity models predict fish diversity patterns in Mississippi-Missouri basin. *Nature*, **453**, 220–222.
- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.
- Petersen, I., Winterbottom, J.H., Orton, S., Friberg, N., Hildrew, A.G., Spiers, D.C. & Gurney, W.S.C. (1999) Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. *Freshwater Biology*, **42**, 401–416.
- Petersen, I., Masters, Z., Hildrew, A.G. & Ormerod, S.J. (2004) Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology*, **41**, 934–950.
- Poff, N.L. (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, **16**, 391–409.
- Poff, N.L. & Ward, J.V. (1995) Herbivory under different flow regimes -a field experiment and test of a model with a benthic stream insect. *Oikos*, **72**, 179–188.
- Poff, N.L., Wellnitz, T. & Monroe, J.B. (2003) Redundancy among three herbivorous insects across an experimental current velocity gradient. *Oecologia*, **134**, 262–269.
- Shurin, J.B. & Allen, E.G. (2001) Effects of competition, predation, and dispersal on species richness at local and regional scales. *The American Naturalist*, **158**, 624–637.
- Soininen, J., Lennon, J.J. & Hillebrand, H. (2007a) A multivariate analysis of beta diversity across organisms and environments. *Ecology*, **88**, 2830–2838.
- Soininen, J., McDonald, R. & Hillebrand, H. (2007b) The distance decay of similarity in ecological communities. *Ecography*, **30**, 3–12.
- Starzomski, B.M. & Srivastava, D.S. (2007) Landscape geometry determines community response to disturbance. *Oikos*, **116**, 690–699.
- Thompson, R.M. & Townsend, C.R. (2006) A truce with neutral theory: local deterministic factors, species traits and dispersal limitation determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology*, **75**, 476–484.
- Townsend, C.R. (1989) The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, **8**, 36–50.
- Urban, M.C. (2004) Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology*, **85**, 2971–2978.

Received 29 September 2009; accepted 11 January 2010

Handling Editor: Lennart Persson