

# Distance decay of similarity in temperate aquatic communities: effects of environmental transition zones, distance measure, and life histories

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The decay of community similarity with distance (distance decay) is reported for many taxa in a variety of geographic settings. However, the importance of scale, distance measure, ecoregions, and ecological transition zones to distance decay has not been thoroughly examined. The goal of our study was to test the effects of these factors on distance decay in two freshwater assemblages (benthic macroinvertebrates and fish) with differing dispersal abilities in small streams within the Patuxent River basin, Maryland, USA. The Patuxent basin contains a geologic Fall Line, an ecological transition zone separating the two main regions of the basin. For both assemblages, we examined distance decay in similarity at several extents: entire Patuxent, Piedmont sub-region, and Plains sub-region using both linear geographic and stream network distances. Decay patterns were observed across all extents and distances. At the Patuxent extent decay rates differed between linear and stream distance only for macroinvertebrates (linear > stream); with both distance measures, similarity in fish decayed faster than similarity in macroinvertebrates. Within the Plains, decay rates for macroinvertebrates were lower than at the Patuxent for both distance measures; no difference in decay rates for this assemblage were detected in the Piedmont. Decay rates of similarity for fish only differed (lower) from rates at the Patuxent when examined at the Piedmont extent with stream distance. Similarity for the subset of sites that were located in separate ecoregions decayed at a slower rate than similarity for the entire data set only for macroinvertebrates with linear distance, suggesting a weak effect of the transition zone on distance decay. Together, these results suggest multiple factors contribute to the distance decay pattern and therefore regional diversity patterns, suggesting conjoint examination of these factors will further our understanding of the mechanisms governing regional diversity patterns.

Studies in spatial ecology have shown how diversity and distribution patterns at large continental scales are affected by evolutionary-driven processes (Lomolino et al. 2009). A pattern consistently shown in biogeographic studies is a decrease in community similarity with increasing distance between two sampled sites (distance decay; Nekola and White 1999, Soininen et al. 2007, Jobe 2008). This decay is a manifestation of processes controlling community composition that operate across a gradient of scales. Community similarity at large scales tends to decrease with distance due to factors including decreased environmental similarities, dispersal limitations, and niche width differences (Nekola and White 1999). Conversely, classic experimental studies in ecology have shown that at relatively small scales, processes such as competition and predation drive diversity patterns (Ricklefs and Schluter 1993) and thus disturbance regimes and species interactions are important in determining species composition at these scales (Ricklefs and Schluter 1993, Mouquet et al. 2003, Munguia 2004). There is also recognition that at some intermediate scale, which can be taxa or habitat specific, both biogeographic

and ecological mechanisms will shape diversity and it is at this scale that a mechanistic understanding of patterns of distance decay may be revealed (sensu Harrison and Cornell 2008). Intermediately scaled studies also enable the examination of how species' natural histories and environmental transition zones (e.g. boundaries between two distinct regions) affect large scale patterns in species composition, such as distance decay. However, reconciling these scales, identifying diversity patterns, and the underlying processes has been a daunting task (Holt 1993).

Distance decay often is examined using linear geographic (hereafter linear) distance; however the decay pattern also may occur with other distance measures or environmental gradients. For example, vegetation patterns are strongly controlled by elevation (Jacquelyn et al. 2005) and community structure shifts along salinity gradients (Sosa-Lopez et al. 2007), therefore distance measures based on these environmental variables may better elucidate the distance decay relationship. In streams, communities are strongly influenced by the dendritic structure of streams (Grant et al. 2007), thus a distance measure based on this

factor (e.g. stream distance) may be an appropriate venue to examine distance decay. When examined conjointly, a comparison of the distance decay pattern using the traditional linear distance and an alternative distance measure based on an environmental distance will enable an assessment of how these factors affect regional species composition patterns (Steinitz et al. 2006, Blanchette et al. 2008).

Studies at intermediate scales also enable an examination of the effects of environmental transition zones between regions (i.e. ecotones) on the distance decay pattern. These zones are areas of rapid change in conditions and fauna relative to the spatial extent of adjoining regions (Odum 1997) so they may exert a strong effect on the decay pattern. Boundaries between adjacent ecoregions are one such intermediately-scaled transitional zone. Ecoregions are geographical areas similar in climate, physiography, landform, soils, vegetation, and hydrology (Omernik 1987). The boundaries between these regions separate dissimilar areas and the possibly different communities within them. Thus, these boundaries may constrict differential community composition and thus strongly affect distance decay. For example, ecoregion boundaries between biomes and major geographical features (e.g. mountains) have higher turnover of trees, birds, and mammals than related within-ecoregion turnover (McDonald et al. 2005). However, the effect of transition zones on distance decay patterns in other taxonomic groups is unknown.

In freshwater streams, benthic macroinvertebrates and fish are two dominant taxonomically and functionally diverse assemblages. Benthic macroinvertebrate assemblages often reach genus-level richness values over 40 per stream and densities well above 1000 m<sup>-2</sup> of streambed area (Benke et al. 1984, Moore and Palmer 2005), and include a variety of life history strategies (Merritt and Cummins 1996, Wallace and Webster 1996). Fish assemblages also usually include a variety of different life history strategies (Schlosser 1982, Schleiger 2000) and although have lower densities than benthic macroinvertebrates (e.g. often < 50 m<sup>-2</sup>, Schlosser 1987), they usually are diverse (e.g. 10–20 species per stream, Schlosser 1985, Marsh-Matthews and Matthews 2000). Both benthic macroinvertebrates (Petersen et al. 2004) and fish (Matthews and Robison 1998) use stream corridors as a dispersal medium, therefore, both assemblages may exhibit a faster decay signal with measures of stream network (hereafter stream) distance than linear distance. However, reliance on stream corridors likely differs between these two taxonomic groups. For example, the aerial life stages of many aquatic insects (Sheldon 1984, Bunn and Hughes 1997) may reduce their dependence on corridors for dispersal. Thus, fish assemblages may show a faster decay with stream distance, whereas macroinvertebrate assemblages may show a faster decay with linear distance. Both assemblages also are heavily influenced by regional factors, such as the ecoregion in which they reside, such that assemblages in adjacent ecoregions are often compositionally different (Hughes et al. 1987, Feminella 2000). Because both fish and aquatic macroinvertebrate assemblages are highly diverse and influenced by the same regional effects, yet differ in dispersal mechanisms, they are excellent models to examine regional-scaled patterns in biodiversity, such as distance decay.

In this study we examine the decay of similarity in benthic macroinvertebrate and fish assemblages within streams of the Patuxent River basin, Maryland, USA. This basin is transected by a geologic Fall-Line separating two ecoregions, the Northern Piedmont (hereafter Piedmont extent) and the Southeastern Plains (hereafter Plains extent). Our first hypothesis is that for the entire Patuxent basin (hereafter Patuxent) and each ecoregion (Piedmont and Plains) similarity in both benthic macroinvertebrates and fish will exhibit the distance decay pattern with both linear and stream distances. Second, due to their aerial dispersal ability macroinvertebrates will show a faster decay signal with linear distance, while fish will show a faster decay signal with stream distance. Third, we expected the relative homogeneity of the environment within ecoregions (cf. between ecoregions) to outweigh the effects of scale even though distance decay relationships have been reported to be steeper at smaller scales (Soininen et al. 2007). Thus, we hypothesize that similarity in both assemblages will decay at slower rates when examined separately for each ecoregion of the Patuxent basin. Fourth, we expect the boundary between the Southeastern Plains and Northern Piedmont ecoregions, the Fall Line, to be a strong environmental transition zone. Thus, nearby sites separated by this boundary will have a lower similarity than comparably separated sites within ecoregions, which will weaken all distance decay patterns.

## Methods

### Study site

The Patuxent River basin (Maryland, USA) flows southeast from headwaters in the Piedmont ecoregion through the Plains ecoregion out to the Chesapeake Bay, draining an area of 2260 km<sup>2</sup> (Fig. 1). The climate is humid subtropical with hot, humid summers and chilly to mild winters (Peel et al. 2007). A geologic Fall Line separates the Piedmont ecoregion and the Plains ecoregion of the basin. The Piedmont is characterized by low rounded hills, irregular plains, and open valleys and is underlain by hard Paleozoic metamorphic rocks; the Plains is characterized by lower elevation and relief than the Piedmont (Supplementary material Table S1) and is underlain by unconsolidated Mesozoic and Tertiary sediments (USGS 2008). The Fall Line also is characterized by numerous waterfalls (USGS 2008). Vegetation ranges from Appalachian forests in the Piedmont to oak/hickory/pine southern mixed forests in the Plains ecoregion (Omernik 1987). The Patuxent River drains the area between the cities of Baltimore (Maryland) and Washington (DC).

### Data sets and analyses

Benthic macroinvertebrate and fish data were taken from the Maryland Biological Stream Survey (MBSS). Sampling sites for the MBSS were selected using a probability-based sampling design stratified by major basin and by stream order on a 1:100 000 USGS map (Southerland et al. 2005). For the Patuxent Basin, only reaches that were ≤ 3rd order and that were collected between 1994 and 2003 were

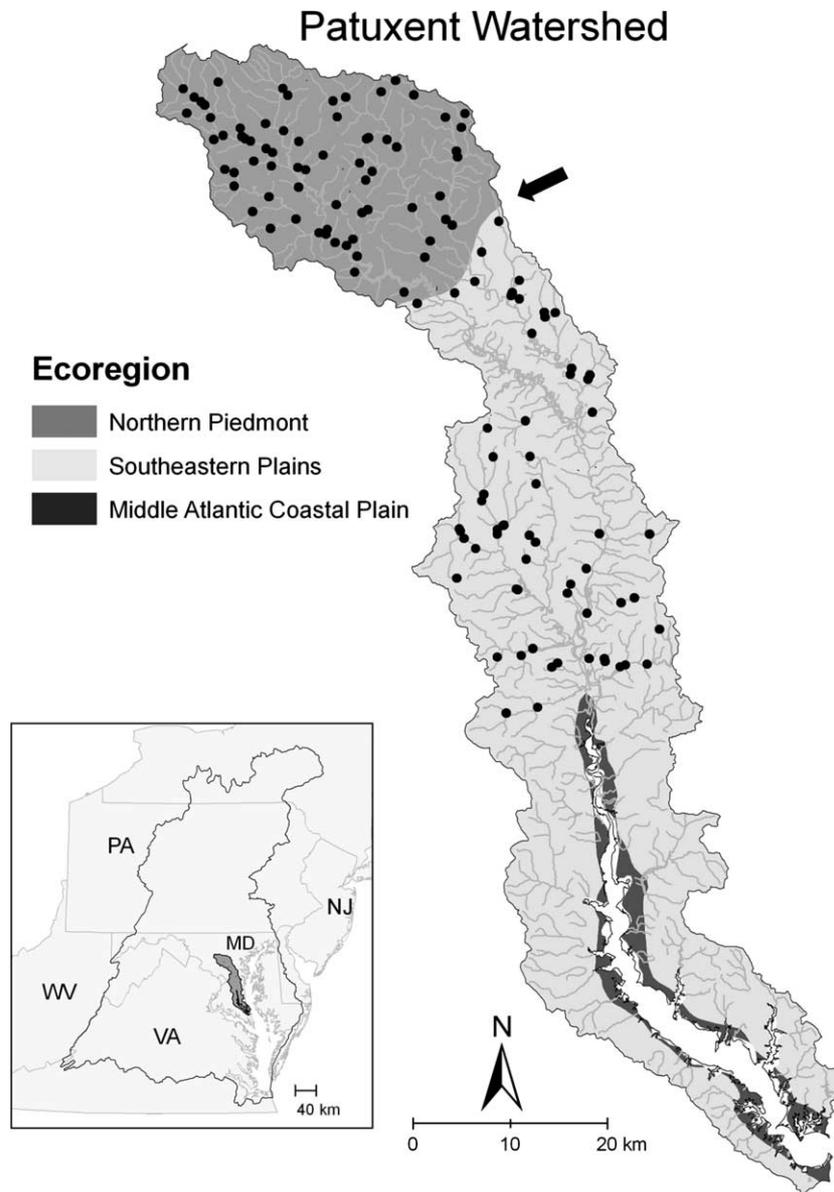


Figure 1. Map of the Patuxent River drainage basin, Maryland, USA, showing its position within the Mid-Atlantic region of the USA (inset), ecoregion boundaries, and locations of stream sampling locations (solid circles). Black arrow indicates approximate location of the geologic Fall Line. MD = Maryland, PA = Pennsylvania, NJ = New Jersey, WV = West Virginia, VA = Virginia.

present in the MBSS database. Benthic macroinvertebrates were sampled in spring with a D-frame net from all habitats over a 75 m stream reach (Klauda et al. 1998), subsampled to 100 organisms, and identified to genus level (Southerland et al. 2005, Supplementary material Table S2). Fish were sampled in summer over the 75 m reach using a double-pass electroshock backpack technique with upstream and downstream block nets; taxa were identified to species level (Kazyak 2001, Supplementary material Table S3).

We restricted our analyses to sites that had direct stream connectivity (i.e. sites from reaches that did not drain directly into the tidally influenced mesohaline and oligohaline waters of the Patuxent estuary (Boynton et al. 2008). Removal of ambiguous taxa (i.e. coarse-level identification, or unknowns) resulted in a  $129 \times 195$  site by taxa matrix for macroinvertebrates and a  $129 \times 50$  site by taxa matrix

for fish. Bray–Curtis similarity between pairs of sites in the Patuxent basin (detailed below) was calculated using the vegan library in the R software package (vegdist function, R, Oksanen et al. 2008). Raw abundance data were root-root transformed prior to similarity analysis to reduce the influence of highly abundant taxa.

We first evaluated the structure of both assemblages with non-metric multidimensional scaling (NMDS, root-root transformed abundance data, Bray–Curtis distance, 3 dimensions). Differences in assemblage structure between the two regions were tested with Multiple Response Permutation Procedures (MRPP, 999 permutations). Both NMDS and MRPP were performed in the R software package using the vegan package (Oksanen et al. 2008).

We examined distance decay of similarity between sites (hereafter referred to simply as “distance decay”) for both

benthic macroinvertebrates and fish by relating community similarity to both linear and stream distance. Linear distance between two sites was calculated by applying the “Distance Between Points” tool in the Hawth’s Tools Extension for ArcGIS (Beyer 2007) to site UTM coordinates from the MBSS database. Stream distance between two sites was calculated by applying the FLOWs extension for ArcGIS (Theobald et al. 2006) using site UTM coordinates and the National Hydrography Dataset plus (NHDplus, <www.horizon-systems.com/nhdplus/index.php>).

To test our first hypothesis, we used simple Mantel analyses (9999 permutations) to test for significant patterns in the similarity and distance matrices at the Patuxent, Plains, and Piedmont extents. We also used partial Mantel tests (9999 permutations) to test for significant patterns between similarity and distance while controlling for environmental effects. The environmental distance matrix was calculated using stream-scaled variables taken from the MBSS (Southerland et al. 2005) and watershed-scale variables taken from previous studies (Maloney et al. 2009; Supplementary material Table S1). The environmental distance matrix was calculated using Euclidean dissimilarity on rescaled data.

Because the ranges in both linear and stream distances varied among analyses, slopes could not be directly compared. Moreover, due to the elongated shape of the Patuxent River watershed observed patterns using all data points also may be affected by edge effects (i.e. sites near edges of the study area have fewer nearby sites than sites located in the middle of the study area, Fortin 1999). Therefore, to test our last three hypotheses we analyzed fixed distance subsets of each data set. We restricted analyses to sites <30 km apart for linear distance and sites <60 km apart for stream distance (resulting sample sizes: Patuxent = 2897, Plains = 1212, Piedmont = 1241, between = 444). These fixed distances assured analyses at each extent (i.e. Patuxent, Plains, Piedmont, and between-ecoregions) had equivalent ranges in the x-axis so that distance decay patterns and decay rate estimates could be compared. Although slightly larger than the recommended ½ minimum extent (Palmer 1988) these restricted distances should reduce edge effects on sample size (Jobe 2008).

To test our second hypothesis, we tested distance decay rates between similarity of assemblages and distance measures for all sites in the entire data set (Patuxent extent). This extent enabled a test of assemblage and distance metric on the general distance decay rate. To test our third hypothesis (ecoregion effect within the Plains and Piedmont), we tested if distance decay rates for the Plains and Piedmont ecoregions of the Patuxent basin differed from those at the Patuxent extent. For these analyses we only used similarities between sites within the same ecoregion (i.e. Plains site vs Plains site or Piedmont site vs Piedmont site) and tested if slopes differed from those at the Patuxent extent. This approach allowed us to compare the distance decay rates of these two assemblages in two adjacent ecoregions. To test our last hypothesis (effect of transition zone), we calculated distance decay rates only for similarities between sites that were located in different ecoregions (i.e. similarities only between Piedmont and Plains sites; between-ecoregions extent). A difference in the distance decay rate with this subset of data compared to the Patuxent

extent analysis would indicate an effect of the transition zone. Because distances and similarities within the data sets were not independent we tested for significant differences between slopes using a randomized permutation test (described in detail in Nekola and White 1999, Steinitz et al. 2006).

## Results

For the entire Patuxent basin the macroinvertebrate assemblage had nearly 4 times the richness of the fish assemblage (195 taxa vs 50 taxa for fish). Total taxa richness at both ecoregion scales also was higher for benthic macroinvertebrates (Piedmont = 167 taxa, Plains = 150 taxa) than fish (Piedmont = 42 taxa, Plains = 40 taxa). Average ( $\pm 1$  SE) local richness was higher for benthic macroinvertebrates than for fish at the Patuxent scale (macroinvertebrates =  $19.9 \pm 0.5$  species, fish =  $11.1 \pm 0.5$  species;  $t = 11.6$ ,  $DF = 243.0$ ,  $p < 0.001$ ) and both ecoregion scales (Piedmont: macroinvertebrates =  $22.5 \pm 0.6$ , fish =  $12.4 \pm 0.6$ ;  $t = 11.6$ ,  $DF = 123.7$ ,  $p < 0.001$  and Plains: macroinvertebrates =  $17.0 \pm 0.8$ , fish =  $9.6 \pm 0.8$ ;  $t = 6.7$ ,  $DF = 109.0$ ,  $p < 0.001$ ). Local richness was higher in the Piedmont than the Plains ecoregion for both macroinvertebrates ( $t = 5.52$ ,  $DF = 101.8$ ,  $p < 0.001$ ) and fish ( $t = 3.23$ ,  $DF = 103.9$ ,  $p = 0.002$ ).

The NMDS for macroinvertebrates reached a convergent solution after 14 iterations and the final stress of the NMDS was 20.3. For fish the NMDS reached a convergent solution after 14 iterations with a final stress of 11.1. Both assemblages visually separated by ecoregion in the first two axes of the NMDS ordinations (Fig. 2; see Supplementary material Fig. S1 for all NMDS plots) and this was confirmed with the MRPP analyses ( $p = 0.001$  for both assemblages).

At the Patuxent extent, linear distances between sites covered a shorter range and had lower mean values than stream distances (Table 1). As expected, the range in linear distance between sampling sites for both the Plains and Piedmont extents was less than that for the Patuxent and between-ecoregions extent data sets (Table 1). The range in stream distance for the Piedmont was comparable to that of the Patuxent and the between-ecoregions extent data sets. At all scales, similarity in the fish assemblages covered a wider range and had higher mean values than similarity in benthic macroinvertebrates.

Similarity of both assemblages appeared to decay with both distance measures at all extents (Fig. 3). Mantel tests supported this as significant patterns were detected in data for both assemblages and both distance measures at the Patuxent, Piedmont, and Plains extents (Table 2). Partial Mantel tests revealed significant patterns for all taxa similarities and distance measures at the Patuxent extent after controlling for environmental distance (Table 2). For the Plains and Piedmont, similarity in benthic macroinvertebrates showed significant patterns with both distance measures after controlling for the effects of environment. However, interestingly similarity in fish only showed a significant pattern with distance for the Plains extent using stream distances following removal of environmental distance effects (Table 2).

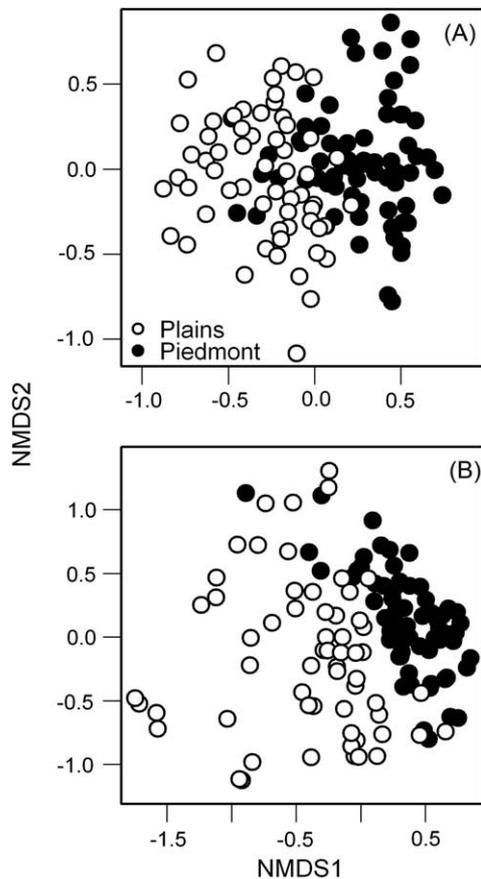


Figure 2. Plots of non-metric multidimensional scaling (NMDS) ordination site scores on axis 1 (NMDS1) vs axis 2 (NMDS2) for (A) benthic macroinvertebrates and (B) fish. Plains = Southeastern Plains, Piedmont = Northern Piedmont.

At the Patuxent extent, the decay rate for benthic macroinvertebrates with linear distances (rate =  $-0.0048$ ) was double that when stream distance was used ( $-0.0024$ ,  $p = 0.063$ ). No difference in decay rates was found for the fish assemblage (linear =  $-0.0066$ , stream =  $-0.0035$ ;  $p = 0.936$ ). Fish decay rates were higher than macroinvertebrate decay rates at this extent for both linear and stream distances (both  $p < 0.001$ ).

Decay rates at both ecoregion extents appeared different from those at the Patuxent extent (Fig. 3A–F). Within the Plains, decay rates with linear distances for macroinvertebrates and fish were significantly less than rates at the Patuxent extent (Table 3). Macroinvertebrate decay rates with stream distance in the Plains were weakly significantly

( $p = 0.075$ ) less than rates at the Patuxent; decay rates with stream distance for fish in the Plains did not differ from decay rates for the Patuxent. At the Piedmont extent decay rates with linear distance for macroinvertebrates and fish were not different from decay rates at the Patuxent extent; decay rates with stream distance for macroinvertebrates did not differ from those at the Patuxent extent, however fish similarity decayed at a slower rate in the Piedmont than the Patuxent (Table 3).

At the between-ecoregions extent, similarity of macroinvertebrates decayed at a slightly slower rate than at the Patuxent extent ( $p = 0.083$ , Table 3). Decay rates at this extent for macroinvertebrates with stream distance, fish with linear distance, and fish with stream distance did not differ from decay rates observed at the Patuxent extent (Table 3).

## Discussion

Originally formulated in the geographic sciences (“First Law of Geography”, Tobler 1970), the concept of distance decay of similarity is inherent in much pioneering ecological research (Whittaker 1960, Preston 1962) and has been reported for a variety of taxa and geographic settings (Brouat and Duplantier 2007, Sojininen et al. 2007, Jobe 2008). Results of our analyses on decay in similarity of fish and macroinvertebrate assemblages in the Patuxent River basin support this general paradigm; however, the decay patterns depended on spatial extent, distance measure (linear or stream distance), and taxonomic group. For example, decay rates at the entire Patuxent extent were often faster than analogous decay rates in the Plains ecoregion but not the Piedmont ecoregion. Moreover, similarity decayed faster with linear distance than stream distance at the Patuxent extent for benthic macroinvertebrates but not fish. When decay rates from the entire Patuxent were compared to rates from the subset of sites that were located in different ecoregions, the only significant difference was that macroinvertebrates decayed at a slightly slower rate at the between-ecoregions extent, indicating a weak effect of the transition zone. Taken together, these results suggest multiple factors contribute to the distance decay pattern and therefore regional stream diversity patterns in the Patuxent basin. However, the differences in taxonomic groups, decay measures, and ecoregions highlight the complexity encountered at intermediate biogeographic scales.

Table 1. Summary statistics for distances and similarities for the four extents. SD = standard deviation, Invert = benthic macroinvertebrates, Between = between-ecoregions.

	Patuxent		Plains		Piedmont		Between	
	Range	Mean (SD)						
Distance (km)								
Linear	0.1–76.7	29.2 (18.6)	0.1–51.3	18.7 (11.1)	0.22–31.1	12.4 (6.4)	1.8–76.7	43.1 (14.6)
Stream	0.1–140.9	71.4 (38.2)	0.1–96.4	40.1 (22.6)	0.3–140.9	63.5 (48.1)	7.5–138.9	89.1 (24.8)
Similarity (0–1.0)								
Invert	0.00–0.69	0.26 (0.11)	0.00–0.64	0.27 (0.10)	0.00–0.69	0.31 (0.11)	0.00–0.68	0.23 (0.10)
Fish	0.00–0.90	0.37 (0.20)	0.00–0.90	0.35 (0.21)	0.00–0.89	0.49 (0.17)	0.00–0.86	0.31 (0.18)

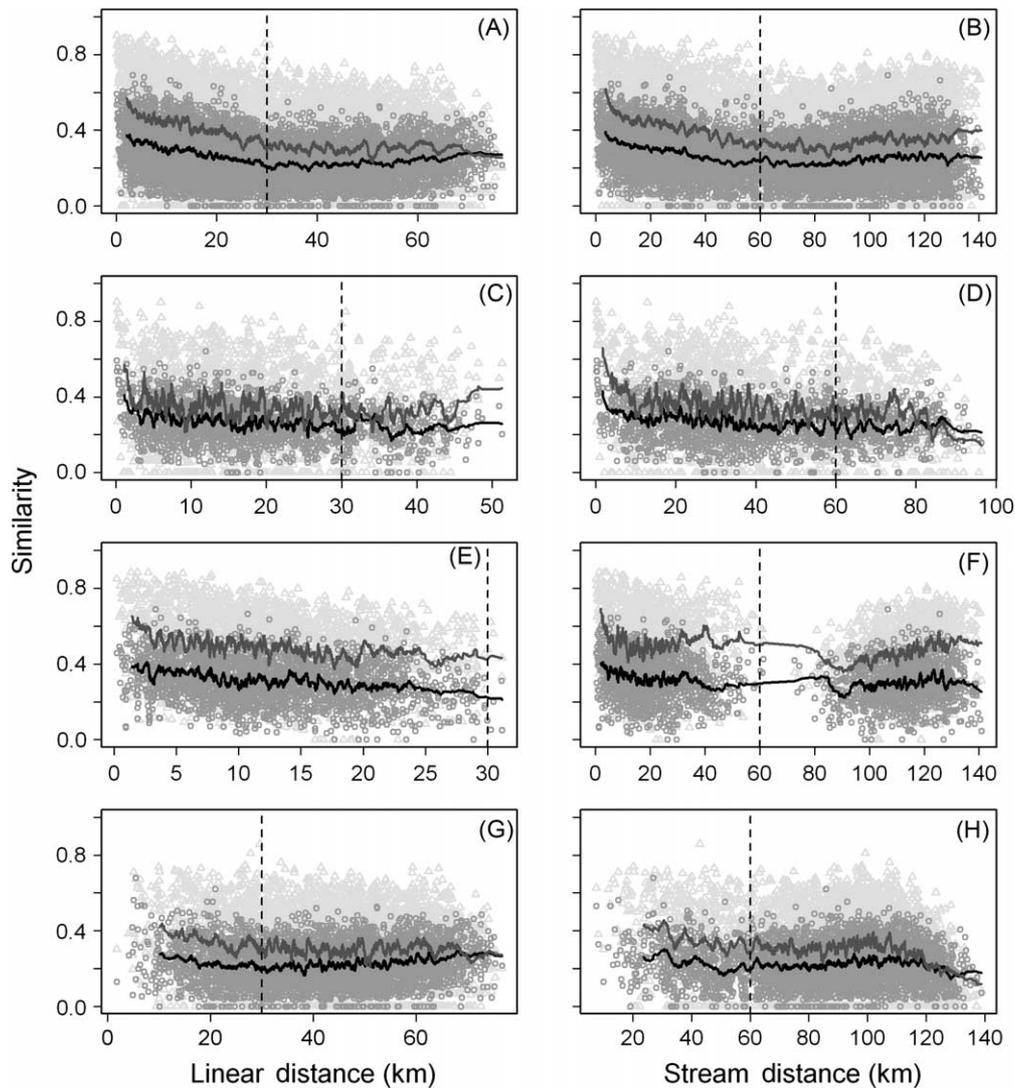


Figure 3. Bray–Curtis similarity of benthic macroinvertebrates (open gray circles) and fish similarities (open light gray triangles) plotted against distances. (A) Similarities vs linear distance for entire Patuxent region, (B) similarities vs stream distance for entire Patuxent region, (C) similarities vs linear distance for Plains ecoregion, (D) similarities vs stream distance for Plains ecoregion, (E) similarities vs linear distance for Piedmont ecoregion, (F) similarities vs stream distance for Piedmont ecoregion, (G) similarities vs linear distance for between-ecoregions analyses, (H) similarities vs stream distance for between-ecoregions analyses. For visual clarity, black lines represent the running average for benthic macroinvertebrates; dark gray lines represent the running average for fish (R library, gregmisc, Warnes 2008). Running window sizes were relative to the total number of similarities in the data set (i.e. the Patuxent scale). For Patuxent-scale analyses the window size was 100, Plains analyses contained about 20% of the similarities thus the window size was 20, Piedmont analyses (30% of observations) had a window size of 30, and between-ecoregions analyses (50% of observations) had a window size of 50. Dashed vertical lines indicate fixed distance subset used in testing differences among slopes (linear distance = 30 km, stream distance = 60 km).

Community diversity patterns are often regulated by more than one factor, including dispersal constraints and environmental barriers (Ricklefs and Schluter 1993). In our study, similarity for both assemblages correlated with linear and stream distance at all extents examined. At the Patuxent extent these correlations remained even after controlling for environmental variation indicating factors other than those included in the environmental distance matrix are controlling species patterns at this scale. However, at the ecoregion scale fish assemblages appeared to be controlled by environmental factors, whereas benthic macroinvertebrates appeared to be controlled by factors other than those included in the environmental distance matrix. This

dichotomy suggests fish are more strongly influenced by environmental factors than associated benthic macroinvertebrate assemblages. However, across the entire study area the control of environmental factors on the fish assemblage relaxed resulting in other mechanisms (e.g. dispersal) exerting stronger controls on this assemblage. A more formal investigation into the roles of dispersal on these assemblages is warranted to substantiate these findings.

### Distance measures, life histories, and distance decay

We expected that both assemblages would exhibit decay patterns with both distance measures; however, due to

Table 2. Results of Mantel and partial Mantel (controlling for environmental similarity) correlation analyses. Boldface highlights non-significant correlations. Invert = benthic macroinvertebrates.

Extent	Taxa group	Distance	Mantel r	p value	Partial Mantel r	p value
Patuxent	Invert	Linear	-0.267	0.0001	-0.196	0.0001
		Stream	-0.184	0.0001	-0.149	0.0001
	Fish	Linear	-0.311	0.0001	-0.227	0.0001
		Stream	-0.194	0.0001	-0.153	0.0001
Plains	Invert	Linear	-0.221	0.0001	-0.207	0.0001
		Stream	-0.208	0.0003	-0.195	0.0001
	Fish	Linear	-0.090	0.0402	<b>-0.057</b>	<b>0.1306</b>
		Stream	-0.186	0.0012	-0.161	0.0032
Piedmont	Invert	Linear	-0.260	0.0001	-0.152	0.0010
		Stream	-0.138	0.0011	-0.104	0.0112
	Fish	Linear	-0.194	0.0004	<b>-0.053</b>	<b>0.1648</b>
		Stream	-0.119	0.0088	<b>-0.077</b>	<b>0.0650</b>

different life histories and thus potential dispersal constraints, benthic macroinvertebrates would show a faster decay pattern with linear distance, whereas the fish assemblage would show a faster decay pattern with stream distance. Our results partially supported these hypotheses as similarity in benthic macroinvertebrates decayed more strongly with linear than stream distance at the Patuxent extent, whereas decay rates in similarity between linear and stream distance did not differ for the fish assemblage. A possible reason for the equivalent decay relationships with linear and stream distances for fish similarity is the dendritic nature of streams within the study area, especially in the Piedmont ecoregion, which had two main tributaries (Fig. 1). This resulted in sites that were relatively close geographically (<20 km) being far apart by stream distance (>100 km). Such close proximity geographically likely resulted in similar environmental conditions that minimized the inhibitory effects of stream distance on fish assemblage similarity. Additionally fish species may have been able to travel the range of stream distance in our study (140 km) because some fish species have been reported to travel such distances in streams (Gowan et al. 1994). Moreover, the environmental transition boundary between the two ecoregions may not have been inhibitory to fish movement patterns. Difficulty separating fish assemblages by ecoregions in close proximity has been reported (McCormick et al. 2000), suggesting that ecoregion boundaries may not be influential in structuring fish assemblages at intermediate scales. Possible directions for future studies into the distance decay pattern in stream

systems (especially for fish) may be to include a larger stream network distance, functional traits (Poff 1997), or multiple ecoregions where stronger boundaries are present (e.g. Plains, Piedmont, Appalachian Mountains).

For most of the distance decay relationships, fish similarity decayed at a faster rate than analogous benthic macroinvertebrates decay patterns. A possible mechanism behind these faster decay rates may be the lower diversity of the fish assemblage because both local and regional diversity affect community similarity (Srivastava 1999, Loreau 2000, Munguia 2004). Fish had lower gamma diversity at the Patuxent and both ecoregion extents. Fish also had lower average local (alpha) diversity at all scales than the benthic macroinvertebrates. It is also possible that in our study area the fish taxa had a greater sensitivity to the environmental heterogeneity compared to the macroinvertebrate assemblage. However, examination of individual species' sensitivities is beyond our study. Differences in taxonomic resolution (i.e. benthic macroinvertebrates identified to genus, fish identified to species) also may have confounded the distance decay patterns. The higher "taxonomic grain" in the macroinvertebrates may have resulted in a higher overlap of species ranges when only considering genera, which could have led to lower decay rates of similarity. However, congeneric aquatic insect taxa (dominant group in the data set, ~95% of collected individuals, Supplementary material Table S2) often have similar life histories and dispersal strategies (Merritt and Cummins 1996), thus differences in taxonomic resolution may not have drastically affected the distance decay comparisons.

Table 3. Decay rates for each assemblage by distance measure and extent of study. Numbers in parentheses are p-values from the randomization procedure testing the difference between each extent's slope from relative Patuxent extent slope - values <0.05 indicate strong evidence for significant difference between slopes, <0.10 weak evidence for differences in slopes. Invert = benthic macroinvertebrates, Between = between-ecoregions.

Taxa group	Distance	Extent			
		Patuxent	Plains	Piedmont	Between
Invert	Linear	-0.0048	-0.0029 (0.042)	-0.0045 (0.494)	-0.0031 (0.083)
	Stream	-0.0024	-0.0015 (0.075)	-0.0017 (0.127)	-0.0022 (0.624)
Fish	Linear	-0.0066	-0.0029 (0.035)	-0.0052 (0.219)	-0.0044 (0.171)
	Stream	-0.0035	-0.0022 (0.121)	-0.0005 (0.008)	-0.0033 (0.774)

## Scale dependence, ecoregions, environmental transition zones, and distance decay

The issue of scale has received much attention from ecologists (Ricklefs and Schluter 1993, Chase and Leibold 2002, Holyoak et al. 2006) and has led to great advances in our understanding of the factors governing species patterns, yet no examination of scale effects on distance decay has been performed. We examined the effects of scale on distance decay by evaluating the decay pattern at several spatially nested extents; first at the entire Patuxent, then for the subset of sites that were located in different ecoregions, and finally by each ecoregion portion of the Patuxent watershed. Here, we hypothesized that similarity in both assemblages would decay at slower rates when examined separately for each ecoregion sub-region of the Patuxent basin. Decay rates were shallower in the Plains than Patuxent for three of the four comparisons (fish similarity with stream distance showed no difference in decay rates), but the only differences found in the Piedmont was a slower decay rate between fish similarity and stream distance. Such differences between ecoregions and taxonomic group highlight different factors controlling the assemblages in each ecoregion. The higher decay rates in the Piedmont (cf. Plains) approximated decay rates observed at the Patuxent extent suggesting turnover within the Piedmont is equivalent to that at the entire Patuxent. These more rapid decay rates in the Piedmont may be a result of a more heterogeneous landscape and thus a higher among-stream variation in stream habitat (Mulholland and Lenat 1992) and different community structure in the Piedmont compared to the Plains (Feminella 2000, Fig. 2). The greater variation would likely cause a more rapid decrease in similarity between two locations than two identically spaced locations in the more homogenous Plains, suggesting a strong control of environment on assemblages in this area.

We found weak evidence for an effect of the environmental transition zone on the distance decay pattern. McDonald et al. (2005) previously found an effect of ecoregion on species turnover for transition zones to occur only between biomes and major geological features. It is possible that the Fall Line did not act as a strong barrier for stream fish and benthic macroinvertebrates in our study area. Rather these communities gradually shifted as one moved across ecoregion boundaries. However, by examining the decay pattern at several extents we have shown that the decay rate varied by scale, assemblage, and distance metric. The next step in understanding how ecoregion boundaries affect regional community patterns would involve addressing the synergistic effect of the evolutionary trajectory of species with the geologic history of habitats; keeping in mind that ecoregion boundaries may shift through geologic history and remnant taxa or isolated populations may confound within-ecoregion studies (Brown and Lomolino 2000). Intermediate spatial scales are grey areas that fall between the realms of biogeography and experimental ecology, yet can provide a wealth of information in understanding the interaction between historical and ecological constraints in shaping species boundaries and community structure. We suggest examining diversity patterns at intermediate scales and conjointly assessing multiple taxonomic groups and dispersal con-

straints (e.g. historical vs ecological constraints) will aid in uncovering the mechanisms driving regional community patterns.

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