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Anthropogenic disturbance and landscape patterns affect diversity patterns of aquatic benthic macroinvertebrates

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Abstract. Measures of species diversity are valuable tools for assessing ecosystem health. However, most assessments have addressed individual sites or regional taxon pools, with few comparisons of differences in assemblage composition within or among regions. We examined the effects of anthropogenic disturbance on local richness (α diversity) and species turnover (β diversity) of benthic macroinvertebrates in small streams within and between 2 ecoregions (Northern Piedmont vs Southeastern Plains ecoregions) of the Patuxent River basin (Maryland, USA). Regional species pools did not differ between ecoregions (Piedmont = 166 taxa, Plains = 162 taxa); however, local richness was lower in the Plains (mean = 17.4 taxa/stream) compared to the Piedmont (mean = 22.2 taxa/stream). When streams were categorized into disturbance classes (low, medium, high), local richness did not differ among categories for either region. However, at the entire Patuxent scale, local richness tended to decrease with % impervious cover in a watershed. Variation in species composition, analyzed with nonmetric multidimensional scaling (nMDS), differed significantly between Piedmont and Plains streams, and Plains streams had higher β diversity than Piedmont streams. When partitioned by disturbance category and region, β diversity differed only between the low-disturbance sites (Plains > Piedmont). Relationships between β diversity and environmental variables varied by region. β diversity was weakly negatively related to % row-crop cover in a watershed at the entire Patuxent scale. For the Piedmont region, β diversity tended to decrease with % forest, % pasture, and % row-crop cover in a watershed. Such negative relationships between β diversity and landuse variables indicate a possible homogenization of the assemblage. The incongruence between diversity measures and composition measures, together with differing effects of anthropogenic land use on β diversity in the 2 regions, emphasizes the need to incorporate both α and β diversity and regional environmental factors in conservation/land management studies.

Key words: beta diversity, alpha diversity, multivariate dispersion, nonmetric multidimensional scaling, ecoregion, scale.

Understanding the effects of anthropogenic stressors on biological diversity is a main emphasis of applied ecological research. However, it is difficult to gain a clear understanding of these effects because species

diversity is governed by multiple, nonanthropogenic factors that operate across a continuum of scales (Ricklefs and Schluter 1993, Karlson and Cornell 1998, Ricklefs 2004). This difficulty is heightened in streams because their configuration in the landscape is hierarchically nested within several scales (Frissell et al. 1986, Hawkins et al. 1993). Local stream assemblages are structured by this configuration because each level acts as a filter on the regional species pool, with a regional species joining a local assemblage only if it possesses species traits that enables it to pass each filter

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(Poff 1997). As a result, natural species turnover (β diversity) is likely to be high between sites. Knowledge of how anthropogenic stressors affect β diversity at a regional scale should provide a better understanding of large-scale changes in biodiversity. However, how anthropogenic disturbance affects β diversity has been addressed directly in few stream studies (but see Passy and Blanchet 2007).

Local- or site-scale diversity (α) and regional-scale diversity (γ) (the regional species pool) are relatively easy to measure and understand, but β diversity (differences in species composition among sites) is harder to understand and has been much debated (Whittaker 1956, Legendre et al. 2005, Tuomisto and Ruokolainen 2006). α and γ diversity have been used regularly in landuse and conservation studies (e.g., Voelz and McArthur 2000, Sponseller et al. 2001), in assessments of anthropogenic stressors on stream diversity (e.g., Strayer et al. 2003), or as metrics in indices of biotic integrity (Barbour et al. 1999). Measures of α diversity have provided enormous amounts of information on the effects of anthropogenic stressors on local stream assemblages, but they do not provide information on among-site variation, an important component of γ diversity. Measures of β diversity can provide information on among-site variation. However, β diversity has been thought of as a potential indicator of ecosystem health only recently (Fournier and Loreau 2001, Ward and Tockner 2001). Authors of few stream studies have directly mentioned measuring β diversity, and most of these have focused on comparing regional and local controls on β diversity (e.g., Heino et al. 2003, Stendera and Johnson 2005, Soininen et al. 2007; but see Urban et al. 2006, Passy and Blanchet 2007). However, stream ecologists often have examined compositional differences among sites with various direct (e.g., canonical correlation analysis [CCA], partial CCA [pCCA]) and indirect (e.g., nonmetric multidimensional scaling [nMDS]) gradient approaches (e.g., Richards et al. 1996, Maloney and Feminella 2006). Thus, they have, in effect, studied β diversity. A more formal examination of anthropogenic stressors on stream assemblage β diversity, when used in tandem with measures on α and γ diversity, would provide a more complete assessment of the effects of anthropogenic stress on stream assemblages.

Measures of β diversity also could help in assessments of the degree of biological homogenization of stream assemblages from anthropogenic stressors. Homogenization of assemblages is of global concern (Vitousek et al. 1997, McKinney and Lockwood 1999) and has been documented for several riverine taxa, including fish, amphibians, and mussels (Duncan and

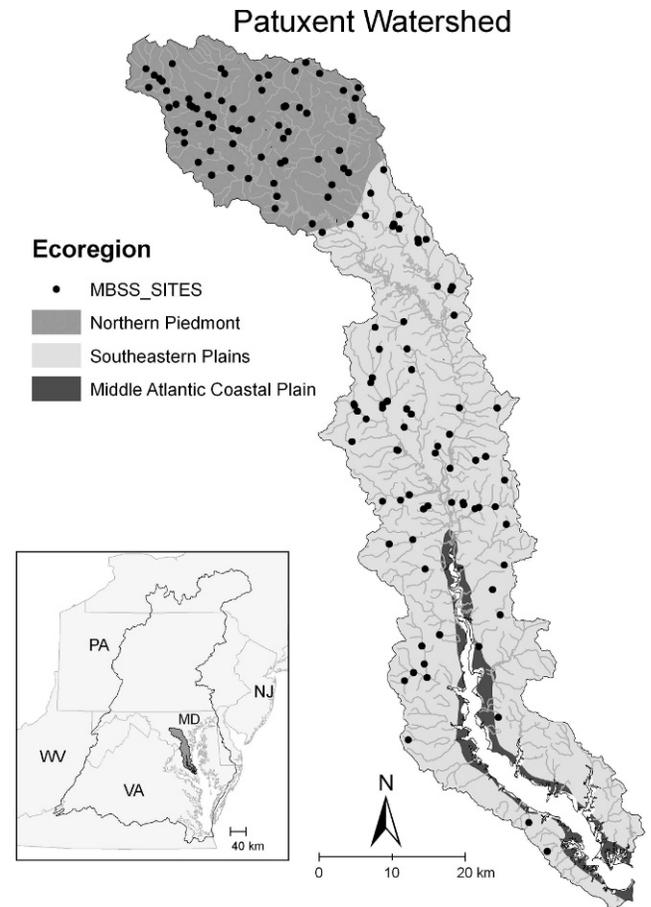


FIG. 1. Stream benthic macroinvertebrate sampling locations and ecoregion boundaries of the Patuxent River drainage basin, Maryland, USA. Inset shows the Patuxent River basin in the mid-Atlantic region of the US and the Chesapeake Bay watershed. MBSS = Maryland Biological Sampling Survey, MD = Maryland, NJ = New Jersey, PA = Pennsylvania, VA = Virginia, WV = West Virginia.

Lockwood 2001, Rahel 2002, Walters et al. 2003). Homogenization occurs from an increase in among-site similarity (i.e., a reduction in β diversity) caused by anthropogenic stressors (e.g., habitat alteration, introductions of non-natives). Therefore, a measure of β diversity would best detect biological homogenization. Estimates of β diversity have been used to identify homogenization of fish assemblages (e.g., Radomski and Goeman 1995). However, we are unaware of past use of β diversity to identify homogenization in stream benthic macroinvertebrate assemblages.

We used a large database of freshwater benthic macroinvertebrates to examine the effects of anthropogenic disturbance on diversity patterns in the Patuxent River basin, Maryland, USA. We first compared α - and γ -diversity patterns of the 2 ecoregions of the Patuxent River basin (Fig. 1). Our

main hypotheses for these analyses were that: 1) γ diversity would be higher for the larger Southeastern Plains region than for the smaller Northern Piedmont region of the Patuxent basin because richness usually increases with area (Preston 1960, MacArthur and Wilson 1967), 2) average α diversity (as taxon richness) would be higher in the region of the Patuxent basin with more in-stream habitat heterogeneity (i.e., Northern Piedmont) because of the positive correlation between habitat heterogeneity and richness (Townsend 1989, Townsend and Hildrew 1994), and 3) α diversity at all scales would decrease with anthropogenic disturbance. Second, we examined β -diversity patterns across the 2 regions. Our main hypotheses were that: 1) β diversity would be higher in the slightly larger Southeastern Plains because dissimilarity between locations increases with distance (Nekola and White 1999), which we postulated would override the effects of local habitat heterogeneity, 2) anthropogenic disturbance would decrease β diversity in both regions of the Patuxent basin because it would result in more homogeneous stream conditions (e.g., Houghton 2007, Poff et al. 2007), and 3) the effects of anthropogenic disturbance on β diversity would differ between regions because assemblages differ between ecoregions (Feminella 2000). Last, we used β diversity to detect if homogenization of benthic macroinvertebrates has occurred in the Patuxent basin because of anthropogenic stress.

Methods

Patuxent watershed

The Patuxent River basin (Maryland, USA) flows in a southeastern direction and drains an area of 2260 km² from its headwaters in the Northern Piedmont ecoregion (hereafter Piedmont region, 617 km²) through the Southeastern Plains ecoregion (hereafter Plains region, 1529 km²) to the Chesapeake Bay (Omernik 1987; Fig. 1). A geologic fall line separates the Piedmont and the Plains regions of the Patuxent basin. The Piedmont region is underlain by crystalline igneous and metamorphic rocks and is characterized by low rounded hills, irregular plains, and open valleys, whereas the Plains region is underlain by unconsolidated sediments and is characterized by lower elevation and relief than the Piedmont (Edwards 1981, USGS 2008). The area has a humid subtropical climate with hot, humid summers and chilly to mild winters (Peel et al. 2007). Vegetation in the Patuxent basin ranges from Tulip Poplar association forests in the upper portions of the basin to Willow–Oak, Loblolly Pine associations in the lower portions. Riparian vegetation consists mainly of River Beach, Sycamore association forests (Brush et al. 1980).

The Patuxent River drains the area between the cities of Baltimore, Maryland, and Washington, DC. Thus, the basin has a high percentage of developed land (19.8% of the total area). Additional dominant land covers within the basin include forested (48.0%), pasture (14.0%), row-crop agriculture (8.8%), and wetland (3.2%) (land cover from the Mid-Atlantic Regional Earth Science Applications Center; RESAC 2000).

Streams within the Plains region are characteristically low gradient with sandy substrates (Felley 1992, Maloney et al. 2005), whereas streams in the Piedmont region show high variability in streambed composition and gradient (Mulholland and Lenat 1992). Thus, among-site variation in habitat (habitat heterogeneity) is likely to be higher in the Piedmont than the Plains. Benthic macroinvertebrate assemblages also differ between the 2 ecoregions (Feminella 2000).

Watershed-scale environmental variables

We used watershed-scale environmental variables to evaluate landscape and anthropogenic disturbance influences on benthic macroinvertebrate diversity patterns across different regional scales. We calculated all watershed-scale environmental variables in ArcGIS (ESRI, Redlands, California). Watershed boundaries came from previous studies (e.g., King et al. 2005), and slope and elevation were calculated from watershed boundaries with a Digital Elevation Model (DEM; 1:250,000 scale, 30 m). We estimated the percentage of each site's entire watershed occupied by row-crop agriculture, wetland, and forest cover from land-cover data classified from ~2000 Landsat TM imagery by the Mid-Atlantic Regional Earth Science Applications Center (RESAC 2000) with classification methods later adopted by US federal agencies for updating the National Land Cover Database (NLCD; Homer et al. 2004). We also calculated % impervious surface within each watershed from an impervious cover map (Goetz and Jantz 2006), developed with subpixel analysis methods that were later adopted for updating NLCD.

Estimates of watershed disturbance

We evaluated the effects of watershed-scale disturbance on macroinvertebrate diversity by 2 methods. First, we grouped sites into 3 disturbance classes based on the amount of impervious surface and row-crop cover in associated catchments, and second, we regressed estimates of α and β diversity on watershed-scale landuse variables (e.g., % impervious surface, % row-crop cover). We used previously published data on the relationship between land use and stream conditions to group sites into disturbance classes. Impairment to biological conditions occurs

between 8 and 15% impervious cover (Paul and Meyer 2001) and between 25 to 50% agricultural cover (Wang et al. 1997, King et al. 2005). Therefore, we assumed the magnitude of the effect of impervious surface was 2× that of agricultural cover and calculated a weighted-average disturbance intensity (DI) as:

$$DI = \frac{2IMP + CROP}{3} \quad [1]$$

where *IMP* is % impervious cover and *CROP* is the % row-crop cover in a watershed. Low-disturbance sites were assigned to $DI < 4$ ($n = 15$ for Piedmont, 18 for Plains), medium-disturbance sites were assigned to $DI = 4$ to 8 ($n = 37$ for Piedmont, 25 for Plains), and high-disturbance sites were assigned to $DI > 8$ ($n = 14$ for Piedmont, 33 for Plains). Categorizing sites into these groups was somewhat subjective, but it provided a useful way to illustrate the utility of β diversity in studies of anthropogenic stressors on stream assemblages. It also serves as an example of use of the method of multivariate dispersion to quantify β diversity (see below).

Stream macroinvertebrate and physicochemical data

Benthic macroinvertebrate data were collected by the Maryland Biological Stream Survey (MBSS; Klauda et al. 1998). This on-going survey uses a probabilistic (random) sampling design stratified by major basin and stream order (1st to 3rd order on a 1:250,000 stream map from 1995–1997 and 1st to 4th order on a 1:100,000 stream map from 2000–2003) where a site consists of a 75-m stream segment. Data collected during this survey included rapid assessment measures of stream physical habitat and hydrology (e.g., discharge, width, depth, velocity, woody debris), water chemistry (e.g., pH, NO₃), and benthic macroinvertebrate assemblages. Benthic macroinvertebrates were sampled in the field during spring with a D-frame net and subsampled in the laboratory with a 100-individual fixed-count method (MD DNR 2005). Macroinvertebrate data were available for 142 sites within the Patuxent River Basin: 76 in the Plains (49 sites in 1997, 5 sites in 2000, 22 sites in 2001), 66 in the Piedmont (31 sites 1997, 19 sites 2000, 16 sites 2002). The data set contained a total of 199 unique taxa after removal of ambiguous taxa (taxa without positive identification). Taxa were identified to the genus level where possible.

Analysis

We used total richness as our measure of α diversity and tested for differences between regions and among

disturbance levels with analysis of variance (ANOVA). We then examined the assemblage structure of the entire Patuxent basin with nonmetric multidimensional scaling (nMDS) on $\log_{10}(x + 1)$ -transformed abundance data and the environmental matrix. nMDS is an indirect gradient analysis technique that uses ranked distances to estimate site (stream) position in species space (McCune and Grace 2002) and is a more robust ordination method than other ordination techniques (Minchin 1987). Differences in assemblage structure (i.e., nMDS scores) between regions and among disturbance classes within regions were tested with analysis of similarities (ANOSIM). ANOSIM is a nonparametric permutation procedure (we used 1000 permutations) that is applied to the rank dissimilarity matrix (Clarke and Warwick 2001). The output from ANOSIM is an *R* statistic that ranges from -1 to $+1$. Most often, the ANOSIM *R* statistic lies between 0 and $+1$, with a value of 0 indicating random grouping and $+1$ indicating that sites within groups are more similar to each other than to sites from different groups (Clarke and Warwick 2001). We also used simple Mantel tests to assess the relationships between environmental distance and benthic macroinvertebrate dissimilarity (Bray–Curtis, 999 permutations). We ran Mantel tests on distance matrices using $\log_{10}(x + 1)$ -transformed abundance data and the environmental matrix (centered to mean and rescaled; see Table 1 for the list of environmental variables). We did all analyses with R statistical software (vegan package; R Core Development Core Team 2008, Oksanen et al. 2008).

We estimated β diversity with the method of multivariate dispersion (Anderson et al. 2006). Multivariate dispersion estimates β diversity as the average dissimilarity (i.e., distance) of sites from their group centroid in multivariate space and has been used to estimate β diversity in riverine fish assemblages (Erös 2007). Here, as an example, we estimated β diversity by multivariate dispersion (R library, vegan, betadisper function) using the first 2 axes of the nMDS ordination. We defined groups at 2 levels, first by ecoregion and then by disturbance category within ecoregion. We analyzed differences in β diversity between regions and disturbance classes within regions with ANOVA.

Use of disturbance classes enables assessment of diversity patterns under different disturbance levels. However, it does not take advantage of the continuous nature of the explanatory variables, which can be used to make inferences on the relationship between environmental variables and macroinvertebrate diversity. Therefore, we regressed α diversity (Poisson generalized linear model) and our measure of β diversity on the environmental predictors. Several

TABLE 1. Mean (\pm SE) values of watershed-scale and in-stream variables in stream reaches of the Patuxent River basin. Analysis of variance (ANOVA) tested differences between Plains and Piedmont regions of the Patuxent River basin and among streams within regions. For watershed-scale ANOVAs, watershed area, slope, and elevation were $\log(x)$ -transformed and % land-cover variables were arcsine(\sqrt{x})-transformed prior to analyses. For instream ANOVAs, all variables were $\log(x)$ -transformed prior to analyses except for woody debris which was \sqrt{x} -transformed. Precipitation and pH were not transformed.

| Variable | Abbreviation | Piedmont | Plains | F | p |
|--|-----------------|-------------|-------------|-------|--------|
| Watershed | | | | | |
| Watershed area ^a (km ²) | Area | 21.2 (3.8) | 12 (1.8) | 3.58 | 0.061 |
| Slope ^a (%) | Slope | 4.0 (0.2) | 3.1 (0.1) | 21.19 | <0.001 |
| Elevation (m) | Elev | 170.3 (3.4) | 51 (2.3) | 764.9 | <0.001 |
| % impervious surface ^a | Imp | 3.5 (0.6) | 8.3 (1.1) | 11.7 | <0.001 |
| % wetland ^a | Wet | 0.4 (0.0) | 0.9 (0.1) | 5.15 | 0.025 |
| % forest ^a | For | 30.2 (1.3) | 47.0 (2.0) | 45.54 | <0.001 |
| % row crop ^a | Crop | 12.3 (1.2) | 8.9 (0.9) | 6.17 | 0.014 |
| % pasture ^a | Past | 29.7 (1.6) | 11.6 (1.1) | 84.59 | <0.001 |
| Precipitation (cm) | Precip | 114.6 (0.1) | 112.2 (0.1) | 233.6 | <0.001 |
| % sand in soils ^a | Sand | 28.1 (0.2) | 42.5 (0.8) | 282.4 | <0.001 |
| In-stream | | | | | |
| Discharge (m ³ /s) | Flow | 2.22 (0.32) | 1.22 (0.18) | 8.04 | 0.005 |
| Width (m) | Width | 4.89 (0.38) | 3.06 (0.22) | 16.44 | <0.001 |
| Depth (cm) | Depth | 30.0 (2.0) | 25.1 (2.0) | 5.21 | 0.024 |
| Flow velocity ^a (m/s) | Veloc | 0.12 (0.01) | 0.12 (0.01) | 0.26 | 0.611 |
| Woody debris ^a (number of pieces) | Wood | 3.6 (0.4) | 5.1 (0.6) | 2.5 | 0.116 |
| NO ₃ (mg/L) | NO ₃ | 2.59 (0.14) | 0.81 (0.06) | 110.0 | <0.001 |
| pH ^a | pH | 7.19 (0.04) | 7.02 (0.07) | 4.91 | 0.028 |

^a Environmental variables used in regression analyses

environmental variables were removed before analyses because of high correlation ($r > 0.60$) with other predictors (e.g., flow, width, and depth were all highly correlated with watershed area; see Table 1 for a list of predictors tested in models).

Results

All watershed-scale variables differed between regions because watersheds within the Piedmont had steeper slopes and higher elevations than watersheds within the Plains region (Table 1). Watersheds in the Piedmont region also had lower % impervious surface, % wetland, and % forest cover than watersheds in the Plains region, but watersheds in the Piedmont region had higher % row-crop and % pasture cover than watersheds in the Plains region. Watersheds in the Piedmont region also received higher amounts of annual precipitation and had lower % sand in soils (Table 1). Streams in the Piedmont region were, on average, larger than those in the Plains region and had higher stream discharges, widths, and depths. Streams in the Piedmont region also had higher levels of NO₃ and pH than streams in the Plains region.

The Plains region of the Patuxent basin is larger than the Piedmont region, but both regions had similar γ diversity. The Piedmont region had 166

taxa, whereas the Plains region had 162 taxa. α diversity differed significantly between regions (greater in the Piedmont [mean = 22.2 ± 0.59 SE] than in the Plains [mean = 17.4 ± 0.64]; 2-way ANOVA, $F_{1,136} = 29.37$, $p < 0.0001$) but not among disturbance levels ($F_{2,136} = 1.87$, $p = 0.16$), and the disturbance \times region interaction was not significant ($F_{2,136} = 1.03$, $p = 0.36$) (Fig. 2). α diversity for the entire Patuxent basin was negatively related to % impervious cover, % sand content in soils, and mean flow velocity and was marginally positively related to abundance of woody debris (Table 2). For Plains streams, α diversity increased with watershed area and decreased with % sand content in soils. For Piedmont streams, α diversity decreased with flow velocity (Table 2). For Plains and Piedmont streams, α diversity was marginally positively related to % pasture cover.

The nMDS reached a convergent solution after 39 iterations, and the 3-dimensional solution had a final stress level of 19.66. Vectors of environmental variables, other than % wetland cover, average flow velocity, and abundance of woody debris, were all significant ($p < 0.05$). Piedmont and Plains site scores were separated along all 3 axes (Fig. 3A–C). The environmental vectors suggest this separation was a result of local (e.g., depth, width), watershed (e.g., % forest cover, watershed area, NO₃, pH), and regional

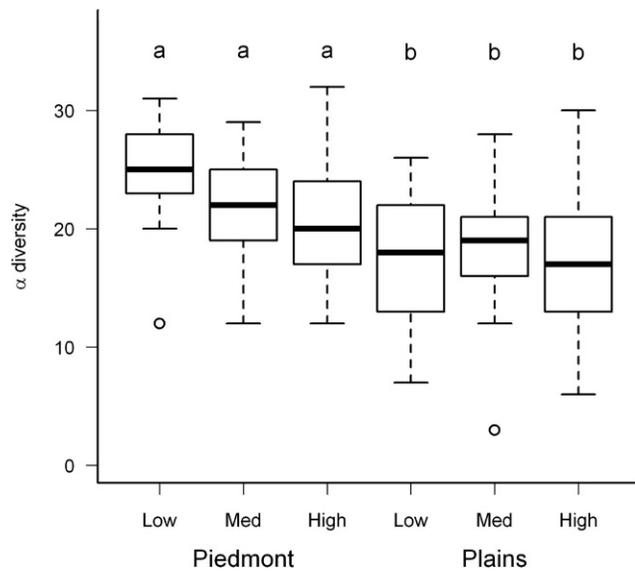


FIG. 2. Box-and-whisker plots for local taxonomic richness (α diversity) by ecoregion and anthropogenic disturbance category. Horizontal lines in box plots show medians, bottoms and tops of boxes show 25th and 75th percentiles, whiskers show ranges, open circles show outliers. Plots with the same letter are not significantly different (analysis of variance). Med = medium.

(e.g., precipitation, % sand content in soils, elevation) factors (Fig. 3A–C, Table 3). Mantel tests indicated significant increases in dissimilarity with environmental distance at the Patuxent (Mantel $R = 0.36$, $p < 0.001$), Piedmont (Mantel $R = 0.30$, $p < 0.001$), and Plains (Mantel $R = 0.36$, $p < 0.001$) scales. β diversity (as measured by distances to respective centroids and

associated convex hulls) appeared different between regions (Fig. 4A), and this difference was confirmed by the multivariate dispersion analysis. Points associated with streams in the Plains region had a higher dispersion (0.46 ± 0.03) than points associated with streams in the Piedmont region (0.36 ± 0.02) (ANOVA, $F_{1,140} = 6.83$, $p = 0.010$; Fig. 4B). Differences in β diversity among combinations of disturbance classes and regions were not as obvious (Fig. 4C). ANOVA indicated a significant difference ($F_{5,136} = 2.78$, $p = 0.020$), but the only statistically significant pairwise difference was between low-disturbance sites in the Piedmont and low-disturbance sites in the Plains (Tukey's Honestly Significant Difference test, $p < 0.05$; Fig. 4D). Average distance to centroids in the medium and high-disturbance sites did not differ between regions or their respective low-disturbance categories.

Distance to centroid for the entire Patuxent scale increased with stream velocity and was marginally negatively related to % row-crop cover in a watershed and pH (Table 2). No significant relationship was found between any environmental predictor and distance to centroid for points representing streams in the Plains region. For points representing streams in the Piedmont region, distance to centroid decreased with % forest, % row crop, and % pasture covers in a watershed and increased with stream velocity (Table 2).

Discussion

Diversity patterns are probably changing because of the heavy influence of anthropogenic stressors on

TABLE 2. Regression coefficients and R^2 for relationships between α diversity and β diversity (measured as distance to centroids of nonmetric multidimensional scaling [nMDS] sites scores [by region]) and environmental variables. For the Patuxent β -diversity analysis, distances were measured from the position (axes 1 and 2) of the ordination point for a sampling site to their respective regional centroid. R^2 values for α diversity are Pseudo R^2 values from the Poisson generalized linear models. R^2 values for β diversity are adjusted R^2 values from linear models. Bold indicates $p < 0.05$, italics indicates $p < 0.10$.

| Variable | α diversity | | | β diversity | | |
|----------------------|--------------------|---------------|---------------|-------------------|--------|---------------|
| | Patuxent | Plains | Piedmont | Patuxent | Plains | Piedmont |
| R^2 | 32.1 | 25.4 | 30.7 | 0.15 | 0.19 | 0.28 |
| Intercept | 3.380 | 2.979 | 3.893 | 1.006 | 0.255 | 1.049 |
| Watershed area | 0.000 | 0.005 | −0.001 | 0.000 | 0.001 | 0.001 |
| Slope | −0.022 | −0.010 | −0.030 | −0.015 | −0.034 | 0.013 |
| % impervious surface | −0.010 | −0.007 | 0.006 | 0.004 | 0.008 | −0.002 |
| % wetland | −0.014 | −0.021 | 0.042 | −0.007 | −0.004 | −0.010 |
| % forest | 0.000 | 0.002 | 0.005 | 0.000 | 0.005 | −0.011 |
| % row crop | 0.001 | 0.005 | 0.001 | <i>−0.005</i> | −0.008 | −0.006 |
| % pasture | 0.004 | <i>0.009</i> | <i>0.007</i> | −0.003 | 0.004 | −0.009 |
| % sand in soil | −0.010 | −0.012 | −0.018 | 0.000 | 0.004 | 0.024 |
| Flow velocity | −0.626 | −0.093 | −1.329 | 0.492 | 0.398 | 0.655 |
| Woody debris | <i>0.009</i> | 0.001 | −0.002 | 0.001 | 0.000 | 0.012 |
| pH | 0.006 | 0.023 | −0.055 | <i>−0.076</i> | −0.032 | −0.118 |

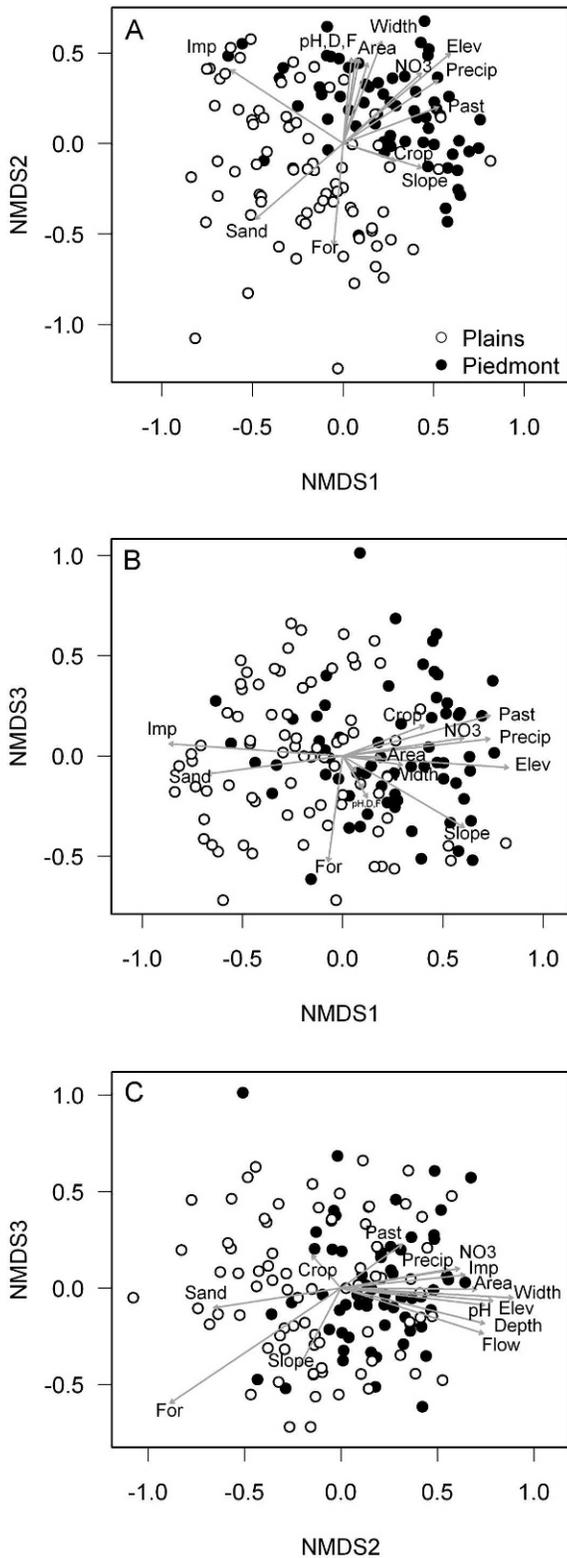


FIG. 3. Plots of nonmetric multidimensional scaling (nMDS) ordination scores on axis 1 vs axis 2 (A), axis 1 vs axis 3 (B), and axis 2 vs axis 3 (C). See Table 1 for variable abbreviations. In panels A and B, D = depth and F = flow. Arrows represent fitted vectors for environmental variables.

TABLE 3. Pearson correlations between watershed-scale variables and axis scores from the nonmetric multidimensional scaling (nMDS) analysis of benthic macroinvertebrate assemblage data for the Patuxent River basin. Bold indicates $p < 0.05$ (Bonferroni corrected).

| Variable | nMDS1 | nMDS2 | nMDS3 |
|----------------------|--------------|--------------|--------------|
| Watershed area | 0.14 | 0.40 | 0.00 |
| Slope | 0.42 | -0.12 | -0.20 |
| Elevation | 0.56 | 0.43 | -0.03 |
| % impervious surface | -0.58 | 0.35 | 0.03 |
| % wetland | -0.22 | 0.02 | -0.05 |
| % forest | -0.05 | -0.53 | -0.32 |
| % row crop | 0.27 | -0.08 | 0.08 |
| % pasture | 0.49 | 0.17 | 0.11 |
| Precipitation | 0.49 | 0.30 | 0.05 |
| % sand in soil | -0.46 | -0.36 | -0.05 |
| Flow | 0.09 | 0.43 | -0.12 |
| Width | 0.21 | 0.51 | -0.03 |
| Depth | 0.07 | 0.43 | -0.10 |
| Velocity | -0.01 | 0.03 | -0.12 |
| Woody debris | -0.08 | 0.14 | 0.07 |
| NO ₃ | 0.41 | 0.34 | 0.05 |
| pH | 0.05 | 0.43 | -0.05 |

ecosystems worldwide (Vitousek et al. 1997). Streams are not exempt from the effects of anthropogenic stressors, and many streams are in biologically impaired condition (USEPA 2006). Anthropogenic stressors also are homogenizing (i.e., decreasing β diversity) stream assemblages across the landscape (Rahel 2002). Measures of α diversity are useful in discerning the effects of anthropogenic disturbance on local stream diversity, but measures of β diversity in streams are more useful than local α diversity measures for detecting homogenization (Radomski and Goeman 1995) and recovery from disturbances (Passy and Blanchet 2007). Our results agree, in part, with these findings in that anthropogenic disturbance in our study watersheds affected both α and β diversity. However, the effects were dependent on the scale of the study area and type of land use, results suggesting that joint use of both measures might provide a more holistic view of anthropogenic effects on stream diversity patterns than use of either measure alone.

α - and γ -diversity patterns

We expected to see a larger regional taxon pool in the Plains than in the Piedmont region because the Plains region is larger and the size of the species pool generally increases with area (Preston 1960, MacArthur and Wilson 1967). However, regional species pools in the 2 regions were similar in size. We had difficulty assigning a mechanism to this counterintu-

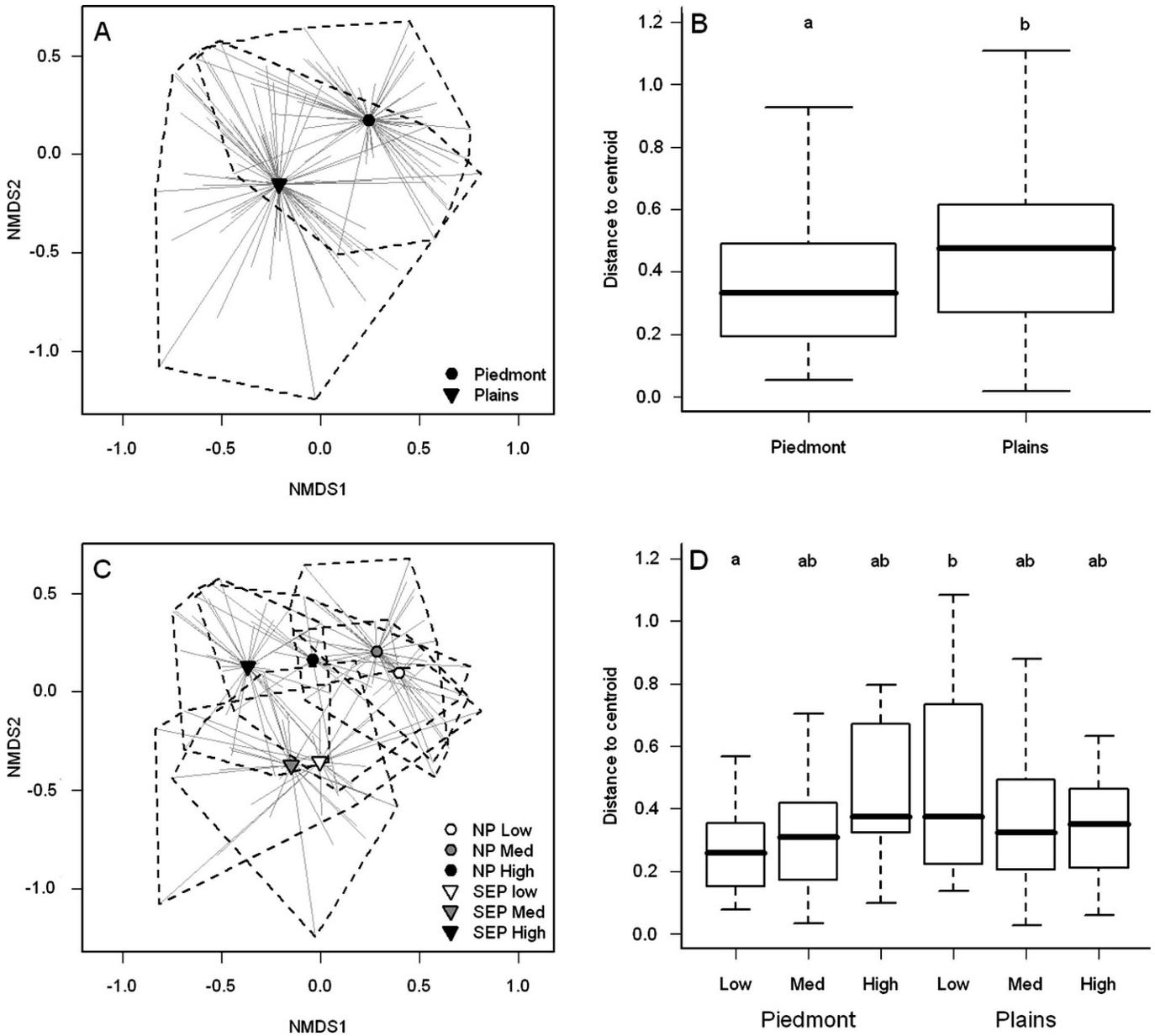


FIG. 4. Plots of ordination scores with convex hulls (dashed lines) and vectors representing the distance from sample location to centroids and estimates of β diversity calculated by multivariate dispersion. A.—Convex hulls and vectors separated by region. B.— β diversity by region. C.—Convex hulls and vectors separated by region and disturbance class. D.— β diversity by region and disturbance class. Horizontal lines in box plots show medians, bottoms and tops of boxes show 25th and 75th percentiles, whiskers show ranges. In panels B and D, plots with the same letter are not significantly different (analysis of variance). Med = medium, NP = Piedmont, SEP = Plains.

itive result, but the pattern might have been a result of the higher α diversity in streams in the Piedmont than in the Plains region. We hypothesized that streams in the Piedmont region might have higher among-stream habitat heterogeneity, which could lead to larger α diversity and thereby counteract the effects of smaller regional area on the regional species pool (Townsend 1989). Streams in the Piedmont region

were, on average, larger than streams in the Plains. However, key habitat factors, such as flow velocity and abundance of woody debris, did not differ between regions. Moreover, examination of coefficients of variation (CV) for habitat variables (e.g., woody debris, discharge, velocity, depth, width) actually suggested that habitat variation was slightly higher among streams in the Plains region than

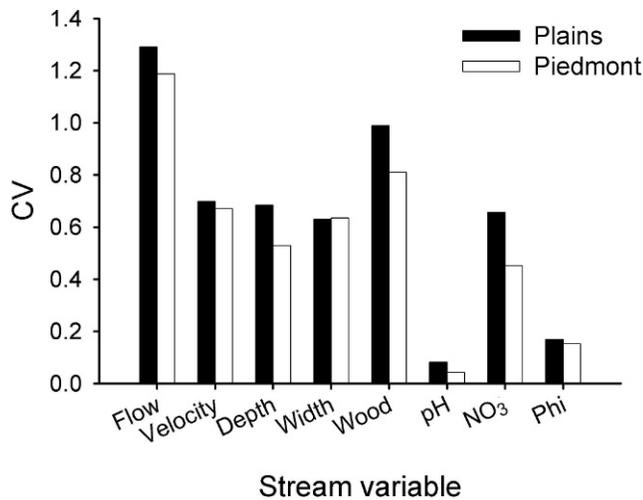


FIG. 5. Coefficients of variation (CVs) for stream habitat variables by region. Phi = Φ scale measure of bed particle size; data were available for only a small subset of streams for this variable (Plains = 27 streams, Piedmont = 35 streams).

streams in the Piedmont region (Fig. 5). Thus, among-site habitat heterogeneity does not appear to be a strong governing mechanism behind the higher α diversity in the Piedmont. Local habitat heterogeneity is an important factor regulating α diversity in streams (Brown 2003). Within-stream heterogeneity could have been higher in the Piedmont than the Plains region, and this difference might explain the higher taxon richness in the Piedmont region. However, within-stream habitat data were not available for our study.

We expected disturbance to decrease α diversity at all scales because of the strong effects of anthropogenic disturbances on benthic assemblages (Barbour et al. 1999). Our results supported this hypothesis at the Patuxent scale because α diversity decreased with % impervious surface. However, we were unable to detect the effects of disturbance (measured as changes in total taxon richness) at the regional scale. Nevertheless, anthropogenic disturbance probably is affecting the assemblages in the Plains and Piedmont regions. For example, the difference in relative abundance of Ephemeroptera, Plecoptera, and Trichoptera (generally sensitive aquatic insect taxa; Barbour et al. 1999) between low and medium-disturbance sites was greater in Plains streams (38.2–21.0, 45.0% loss) than in Piedmont streams (52.8–43.8, 17.1% loss). Losses of sensitive taxa in the Plains might be a reflection of the importance of coarse woody habitat in sandy-bottom streams of the Plains (Smock et al. 1989). This habitat is reduced by anthropogenic disturbance in upslope watersheds (Maloney et al. 2005). In addition, our inability to

detect a disturbance effect at the regional scale could have been a consequence of our use of a small subsample size (100 individuals), which is likely to produce underestimation of actual richness values. Rarefaction analysis (Magurran 1988) showed that the regions had overlapping values for species richness when sample sizes were 100 individuals/site, but neither region was at saturation, a result indicating underestimation of richness. Underestimation is likely to be greater in more diverse (i.e., less disturbed) streams. Thus, our results are conservative and probably reduced our ability to detect an effect of anthropogenic disturbance on the benthic assemblages.

β -diversity patterns

We expected a higher β diversity in the larger Plains region because assemblage similarity between 2 sites decreases with distance between sites (Nekola and White 1999). Thus, larger surveyed areas often have a greater average dissimilarity between sites (i.e., β diversity) than do smaller surveyed areas. The difference in area between the Plains and Piedmont regions probably explains, in part, the higher β diversity among streams in the Plains than in the Piedmont region. The area of the Plains region was $\sim 2.5\times$ larger than that of the Piedmont region. Thus, sites in the Plains region were further apart geographically than sites in the Piedmont (Fig. 1), and greater environmental heterogeneity within the Plains might be a mechanism behind the higher β diversity in the Plains region. Macroinvertebrate dissimilarity showed a stronger relationship with environmental distance in the Plains than in the Piedmont ecoregion and provides support for this explanation.

The effect of distance on β diversity also was evident when sites were partitioned by disturbance category because the low-disturbance streams in the Plains region had a higher β diversity than low-disturbance streams in the Piedmont region. Disturbance was minimal at sites in low-disturbance streams in both regions, so the dissimilarity probably was a result of differences in natural environmental variables. The distance–decay of similarity relationship is a likely mechanism for the difference in β diversity. Low-disturbance sites were, on average, further from their group centroid in the Plains (0.57 ± 0.06 SE) than in the Piedmont (0.31 ± 0.04) region ($t_{30,2} = 3.73$, $p < 0.001$). However, within both regions, medium and high-disturbance sites did not differ from each other or their respective low-disturbance sites. This result suggests that anthropogenic disturbance weakens the distance–decay effect and might indicate homogenization of the assemblages. How-

ever, future studies that directly test this result are needed to support this conclusion.

The relationship between distance to centroid (β diversity) and predictor variables varied with the scale of observation, a result suggesting that measures of β diversity and the effects of anthropogenic disturbance on β diversity are context dependent. For example, significant negative relationships between β diversity and land use were found in the Piedmont but not in the Plains ecoregion. This result suggests a stronger influence of land use on benthic macroinvertebrate assemblages in the Piedmont region of the Patuxent basin than in the Plains region and highlights the need to account for regional environmental variation in analyses. Moreover, these results suggest possible homogenization of the assemblage in the Piedmont but not in the Plains region of the Patuxent and indicate an ecoregion-dependent effect of disturbance.

Given the differences in assemblage composition between the 2 regions, we cannot disregard the fact that taxa with different life histories might respond differently to anthropogenic disturbance. Assemblage-wide disturbance levels and life histories interact strongly (Richards et al. 1997, Munguia and Miller 2008). Partitioning the macroinvertebrate assemblage by life-history traits might elucidate additional patterns between diversity and landscape disturbance (Statzner et al. 2001), but this analysis is beyond the scope of our study. Promising options include separating the assemblage into functional feeding groups (Compin and Cereghino 2007) or by habitat preference (Maloney and Feminella 2006).

Summary and conclusions

Our results suggest that local richness (α diversity) and species turnover (β diversity) of benthic macroinvertebrates in small streams of the Patuxent River basin are controlled by both regional and local factors. However, the strength of these factors varies between regions. Moreover, anthropogenic land use affected these measures of diversity differently. α diversity decreased with % impervious surface cover only at the Patuxent scale, and β diversity was negatively related to % pasture and % row cover only in the Piedmont region. The use of both α and β -diversity measures provided a more holistic assessment of anthropogenic stress on stream benthic macroinvertebrate assemblages than use of either measure alone.

To minimize global loss of diversity resulting from anthropogenic stressors (e.g., WWF 2006), landuse managers and conservationists will need techniques that examine diversity patterns from a variety of

viewpoints. We suggest using measures of β diversity in addition to traditional richness/presence-absence techniques. Moreover, assemblages and environmental factors differ among regions, so assemblage responses to anthropogenic stressors probably will vary from region to region. Thus, future studies also must include regional variation in analyses.

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Literature Cited

- ANDERSON, M. J., K. E. ELLINGSEN, AND B. H. MCARDLE. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683–693.
- BARBOUR, M. T., J. GERRITSEN, B. D. SNYDER, AND J. B. STRIBLING. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, second edition. EPA 841-B-99-002. Office of Water, US Environmental Protection Agency, Washington, DC.
- BROWN, B. L. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters* 6:316–325.
- BRUSH, G. S., C. LENK, AND J. SMITH. 1980. The natural forests of Maryland: an explanation of the vegetation map of Maryland. *Ecological Monographs* 50:77–92.
- CLARKE, K. R., AND R. M. WARWICK. 2001. Change in marine communities: an approach to statistical analysis and interpretation. 2nd edition. Plymouth Marine Laboratory, Plymouth, UK.
- COMPIN, A., AND R. CEREGHINO. 2007. Spatial patterns of macroinvertebrate functional feeding groups in streams in relation to physical variables and land-cover in southwestern France. *Landscape Ecology* 22:1215–1225.
- DUNCAN, J. R., AND J. L. LOCKWOOD. 2001. Spatial homogenization of aquatic fauna of Tennessee: extinction and

- invasion following land use change and habitat alteration. Pages 245–257 in J. L. Lockwood and M. L. McKinney (editors). *Biotic homogenization*. Kluwer Academic/Plenum, New York.
- EDWARDS, J. 1981. A brief description of the geology of Maryland. Maryland Geological Survey, Baltimore, Maryland. (Available from: <http://www.mgs.md.gov/esic/brochures/mdgeology.html>)
- ERŐS, T. 2007. Partitioning the diversity of riverine fish: the roles of habitat types and non-native species. *Freshwater Biology* 52:1400–1415.
- FELLEY, J. D. 1992. Medium–low-gradient streams of the Gulf Coastal Plain. Pages 233–269 in C. T. Hackney, S. M. Adams, and W. H. Martin (editors). *Biodiversity of the southeastern United States: aquatic communities*. John Wiley and Sons, New York.
- FEMINELLA, J. W. 2000. Correspondence between stream macroinvertebrate assemblages and 4 ecoregions of the southeastern USA. *Journal of the North American Benthological Society* 19:442–461.
- FOURNIER, E., AND M. LOREAU. 2001. Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape. *Landscape Ecology* 16:17–32.
- FRISSELL, C. A., W. J. LISS, C. E. WARREN, AND M. D. HURLEY. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10:199–214.
- GOETZ, S. J., AND P. JANTZ. 2006. Satellite maps show Chesapeake Bay urban development. *Transactions of the American Geophysical Union* 87:149–152.
- HAWKINS, C. P., J. L. KERSHNER, P. A. BISSON, M. D. BRYANT, L. M. DECKER, S. V. GREGORY, D. A. MCCULLOUGH, C. K. OVERTON, G. H. REEVES, R. J. STEEDMAN, AND M. K. YOUNG. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18(6):3–11.
- HEINO, J., T. MUOTKA, AND R. PAAVOLA. 2003. Determinants of macroinvertebrate diversity in headwater streams: regional and local influences. *Journal of Animal Ecology* 72:425–434.
- HOMER, C., C. Q. HUANG, L. M. YANG, B. WYLIE, AND M. COAN. 2004. Development of a 2001 National Land-Cover Database for the United States. *Photogrammetric Engineering and Remote Sensing* 70:829–840.
- HOUGHTON, D. C. 2007. The effects of landscape-level disturbance on the composition of Minnesota caddisfly (Insecta: Trichoptera) trophic functional groups: evidence for ecosystem homogenization. *Environmental Monitoring and Assessment* 135:253–264.
- KARLSON, R. H., AND H. V. CORNELL. 1998. Scale-dependent variation in local vs. regional effects on coral species richness. *Ecological Monographs* 68:259–274.
- KING, R. S., M. E. BAKER, D. F. WHIGHAM, D. E. WELLER, T. E. JORDAN, P. F. KAZYAK, AND M. K. HURD. 2005. Spatial considerations for linking watershed land cover to ecological indicators in streams. *Ecological Applications* 15:137–153.
- KLAUDA, R., P. KAZYAK, S. STRANKO, M. SOUTHERLAND, N. ROTH, AND J. CHAILLOU. 1998. Maryland Biological Stream Survey: a state agency program to assess the impact of anthropogenic stresses on stream habitat quality and biota. *Environmental Monitoring and Assessment* 51:299–316.
- LEGENDRE, P., D. BORCARD, AND P. R. PERES-NETO. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75:435–450.
- MACARTHUR, R., AND E. O. WILSON. 1967. *The theory of island biogeography*. University Press, Princeton, New Jersey.
- MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey.
- MALONEY, K. O., AND J. W. FEMINELLA. 2006. Evaluation of single- and multi-metric benthic macroinvertebrate indicators of catchment disturbance over time at the Fort Benning Military Installation, Georgia, USA. *Ecological Indicators* 6:469–484.
- MALONEY, K. O., P. J. MULHOLLAND, AND J. W. FEMINELLA. 2005. Influence of catchment-scale military land use on stream physical and organic matter variables in small southeastern plains catchments (USA). *Environmental Management* 35:677–691.
- MCCUNE, B., AND J. B. GRACE. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon.
- MCKINNEY, M. L., AND J. L. LOCKWOOD. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14:450–453.
- MD DNR (MARYLAND DEPARTMENT OF NATURAL RESOURCES). 2005. *Maryland Biological Stream Survey 2000–2004, Volume VI: laboratory, field, and analytical methods*. Monitoring and Nontidal Assessment Division, Maryland Department of Natural Resources, Annapolis, Maryland. (Available from: http://www.dnr.state.md.us/streams/mbss/current_act.html)
- MINCHIN, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107.
- MULHOLLAND, P. J., AND D. R. LENAT. 1992. Streams of the southeastern Piedmont, Atlantic Drainage. Pages 193–232 in C. T. Hackney, S. M. Adams, and W. A. Martin (editors). *Biodiversity of southeastern United States/aquatic communities*. John Wiley and Sons, Inc., New York.
- MUNGUIA, P., AND T. E. MILLER. 2008. Habitat destruction and metacommunity size in pen shell communities. *Journal of Animal Ecology* 77:1175–1182.
- NEKOLA, J. C., AND P. S. WHITE. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26:867–878.
- OKSANEN, J., R. KINDT, P. LEGENDRE, AND B. O'HARA. 2008. The vegan package. R Foundation for Statistical Computing, Vienna, Austria. (Available from: <http://cran.r-project.org/web/packages/vegan/index.html>)
- OMERNIK, J. M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* 77:118–125.

- PASSY, S. I., AND F. G. BLANCHET. 2007. Algal communities in human-impacted stream ecosystems suffer beta-diversity decline. *Diversity and Distributions* 13:670–679.
- PAUL, M. J., AND J. L. MEYER. 2001. Streams in the urban landscape. *Annual Review of Ecology and Systematics* 32:333–365.
- PEEL, M. C., B. L. FINLAYSON, AND T. A. McMAHON. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11: 1633–1644.
- 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., J. D. OLDEN, D. M. MERRITT, AND D. M. PEPIN. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America* 104:5732–5737.
- PRESTON, F. W. 1960. Time and space and the variation of species. *Ecology* 41:612–627.
- R CORE DEVELOPMENT TEAM. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (Available from: <http://www.R-project.org>).
- RADOMSKI, P. J., AND T. J. GOEMAN. 1995. The homogenizing of Minnesota lake fish assemblages. *Fisheries* 20(7):20–23.
- RAHEL, F. J. 2002. Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* 33:291–315.
- RESAC (REGIONAL EARTH SCIENCE APPLICATIONS CENTER). 2000. 2000 land cover map of the Chesapeake Bay watershed. Mid-Atlantic Regional Earth Science Applications Center (RESAC), Department of Geology, University of Maryland, College Park, Maryland. (Available from: <http://www.geog.umd.edu/resac/>)
- RICHARDS, C., R. J. HARO, L. B. JOHNSON, AND G. E. HOST. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology* 37: 219–239.
- RICHARDS, C., L. B. JOHNSON, AND G. E. HOST. 1996. Landscape-scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Suppl. 1):295–311.
- RICKLEFS, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7:1–15.
- RICKLEFS, R. E., AND D. SCHLUTER. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois.
- SMOCK, L. A., G. M. METZLER, AND J. E. GLADDEN. 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* 70:764–775.
- SOININEN, J., J. J. LENNON, AND H. HILLEBRAND. 2007. A multivariate analysis of beta diversity across organisms and environments. *Ecology* 88:2830–2838.
- SPONSELLER, R. A., E. F. BENFIELD, AND H. M. VALETT. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* 46:1409–1424.
- STATZNER, B., A. G. HILDREW, AND V. H. RESH. 2001. Species traits and environmental constraints: entomological research and the history of ecological theory. *Annual Review of Entomology* 46:291–316.
- STENDERA, S. E. S., AND R. K. JOHNSON. 2005. Additive partitioning of aquatic invertebrate species diversity across multiple spatial scales. *Freshwater Biology* 50: 1360–1375.
- STRAYER, D. L., R. E. BEIGHLEY, L. C. THOMPSON, S. BROOKS, C. NILSSON, G. PINAY, AND R. J. NAIMAN. 2003. Effects of land cover on stream ecosystems: roles of empirical models and scaling issues. *Ecosystems* 6:407–423.
- TOWNSEND, C. R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8:36–50.
- TOWNSEND, C. R., AND A. G. HILDREW. 1994. Species traits in relation to a habitat template for river systems. *Freshwater Biology* 31:265–275.
- TUOMISTO, H., AND K. RUOKOLAINEN. 2006. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. *Ecology* 87:2697–2708.
- URBAN, M. C., D. K. SKELLY, D. BURCHSTED, W. PRICE, AND S. LOWRY. 2006. Stream communities across a rural-urban landscape gradient. *Diversity and Distributions* 12: 337–350.
- USEPA (US ENVIRONMENTAL PROTECTION AGENCY). 2006. Wadeable streams assessment: a collaborative survey of the nation's streams. EPA 841-B-06-002. Office of Water, US Environmental Protection Agency, Washington, DC.
- USGS (US GEOLOGICAL SURVEY). 2008. A tapestry of time and terrain: the union of two maps — geology and topography. (Available from: <http://tapestry.usgs.gov/features/14fallline.html>)
- VITOUSEK, P. M., H. A. MOONEY, J. LUBCHENCO, AND J. M. MELILLO. 1997. Human domination of Earth's ecosystems. *Science* 277:494–499.
- VOELZ, N. J., AND J. V. McARTHUR. 2000. An exploration of factors influencing lotic insect species richness. *Biodiversity and Conservation* 9:1543–1570.
- WALTERS, D. M., D. S. LEIGH, AND A. B. BEARDEN. 2003. Urbanization, sedimentation, and the homogenization of fish assemblages in the Etowah River Basin, USA. *Hydrobiologia* 494:5–10.
- WANG, L., J. LYONS, P. KANEHL, AND R. GATTI. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries* 22(6):6–12.
- WARD, J. V., AND K. TOCKNER. 2001. Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology* 46: 807–819.
- WHITTAKER, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26:1–69.
- WWF (WORLD WILDLIFE FUND). 2006. Living Planet Report 2006. World Wildlife Fund for Nature, Gland, Switzerland. (Available from: http://www.panda.org/about_our_earth/all_publications/living_planet_report/)

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