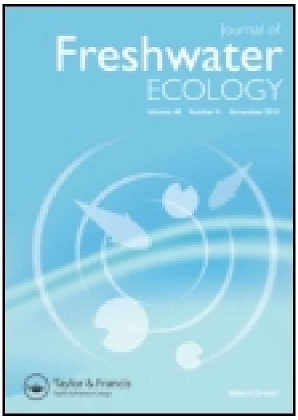

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Effects of disturbance at two spatial scales on macroinvertebrate and fish metrics of stream health

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We analyzed macroinvertebrate and fish assemblage data collected from the upper southeastern coastal plain of the USA to (1) assess the relative sensitivities of bioassessment metrics to in-stream habitat quality, catchment scale land disturbance, and the presence of a reservoir in the catchment and (2) determine whether fish differ from macroinvertebrates in their responses to these variables. Fish and macroinvertebrates responded differently to anthropogenic disturbance: macroinvertebrates were affected most strongly by in-stream habitat quality and fish by the presence of a reservoir in the catchment. Neither taxonomic group were significantly affected by the catchment scale disturbance, probably because the proportions of disturbed land in the study areas were low. Fish may be particularly sensitive to the presence of reservoirs because of their need to cover relatively large distances to complete life cycles and maintain viable populations and because of their sensitivity to the effects of invasive reservoir species, particularly predator fishes. Although not an important predictor in itself, disturbance at the watershed scale was significantly and positively related to in-stream habitat quality, indicating that watershed disturbance had an important indirect effect on aquatic organisms. Direct and indirect ordination showed that the metric data were more strongly related to the disturbance variables than the taxonomic data from which the metrics were derived, possibly because the metrics were less sensitive than the taxon-specific abundances to nondisturbance-related factors. Other factors that may have contributed to this result include greater statistical tractability of the metric data and the relatively high sensitivity of the collective properties represented by the metrics to disturbance-related environmental changes.

Keywords: benthic macroinvertebrates; fish; metrics; streams; spatial scale; disturbance

Introduction

Metrics used for the environmental analysis of aquatic ecosystems are typically biological indicators of community structure or function that are ecologically important and sensitive to environmental disturbances. Metrics and indices composed of metrics (i.e., multimetric indices) are often the basis for bioassessment programs used to infer the ecological health of aquatic ecosystems (Plafkin et al. 1989). Metrics are typically derived from the taxonomic and functional group composition of various groups of organisms such as benthic macroinvertebrates, fish, or diatoms. Important issues concerning

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metrics are their sensitivity to different types of anthropogenic disturbance and to disturbance at different spatial scales. The former topic has been dealt with extensively and is an important factor, along with metric variability, uniqueness, and consistency in selecting metrics for inclusion in multimetric indices (Plafkin et al. 1989; Barbour et al. 1997). The latter topic has been explored less thoroughly. There have been several studies on the effects of environmental variables operating at different spatial scales (e.g., ecoregion, catchment, riparian) on the structure of aquatic communities (Li et al. 2001; Weigel et al. 2003; Johnson et al. 2004), but less effort to explicitly investigate the sensitivity of metrics to disturbance at different spatial scales. Understanding the effects of disturbance at different scales and the effects of such disturbance on metric-based indicators of environmental health can help managers to produce clearer environmental assessments, better identify consequences of different types of disturbance, and determine where to emphasize remediation efforts.

Disturbances that directly affect in-stream habitat would be expected to have a strong influence on stream biota because in-stream habitat constitutes the ambient environment for aquatic organisms. However, physical and biological variables on small spatial scales are affected by factors operating at larger spatial scales. More specifically, stream habitat features are controlled by larger scale geomorphic processes operating at watershed and regional scales (Frissell et al. 1986; Tonn 1990). These linkages are explicitly described by the River Continuum Concept (Vannote et al. 1980) and have been conceptualized as a series of sequential spatial filters that operate to determine stream communities (Poff 1997). Several studies suggest that local-scale factors such as in-stream habitat, current velocity, and water chemistry have a greater influence on macroinvertebrate community composition than larger scale regional factors like catchment land-use (Richards et al. 1997; Johnson & Goedkoop 2002). However, these studies also show considerable unexplained variance in community composition that may be accounted for by the interdependence between local and regional factors. Other studies suggest that disturbances acting at the catchment level have a greater influence on biotic structure than local stream habitat (Stephenson & Morin 2009). The taxonomic group (e.g., fish, macroinvertebrates, diatoms) may influence the results of such studies since different groups may respond differently to disturbance (Paller 2001; Johnson et al. 2006).

This analysis makes use of macroinvertebrate and fish assemblage data collected from stream sites on the upper southeastern coastal plain of the USA that ranged from relatively undisturbed to moderately disturbed. Several biological metrics previously shown to be responsive to environmental disturbance in coastal plain streams were computed from these data. An index of watershed disturbance based on land use as was computed for each site was an index of in-stream habitat quality to represent two spatial scales of disturbance. The objectives of the study were to (1) assess the relative sensitivities of bioassessment metrics to disturbance at the in-stream and catchment scales and (2) determine whether fish and macroinvertebrate assemblages differed in their responses to disturbances occurring at in-stream and catchment scales.

Methods

Study area

Data were collected from first-order through fourth-order streams on the Savannah River Site, a 780 km^2 Department of Energy (DOE) reservation established in 1951 on the upper coastal plain of South Carolina. Soils in this area are mostly sand and loamy sand, while the subsoil textures are usually sandy loam or sandy clay loam. The streams we studied are low gradient, relatively shallow, have a predominantly sandy bottom, and generally lack well-defined pool-riffle-run habitats. Woody debris, such as stumps, logs, twigs, and leaves, constitute the principal in-stream structure, along with aquatic plants, overhanging shoreline vegetation, undercut banks, and root masses. The streams were about 2–15 m wide, 0.6–2.5 m/km in average gradient (i.e., slope between 0.0006 and 0.0025), mildly acidic (pH 4.5–6.9), and relatively low in conductivity (11–104 μS/cm). The relatively low pH and conductivity values in some of the streams were typical of regional blackwater streams and unrelated to anthropogenic disturbance. Streams on the Savannah River Site typically support relatively diverse fish assemblages (7–28 species per site) with many species in the families Cyprinidae, Centrarchidae, Ictaluridae, Percidae, and Catostomidae and diverse macroinvertebrate assemblages (20–55 genera per site) with many taxa in the orders Diptera (primarily Chironomidae), Trichoptera, and Ephemeroptera.

The sample sites represented the upper and middle reaches of the five major stream systems that drain the Savannah River Site into the Savannah River (Figure 1). All sites had substantial flow and none were associated with extensive floodplain swamps as is typical of higher order coastal plain rivers (Benke & Meyer 1988). Some of the streams were largely undisturbed with little or no current agriculture, urbanization, or industrialization in their watersheds, although disturbances of these types occurred prior to 1950. Others had industrial facilities, office buildings, and parking lots in their watersheds or were affected by changes in flow regime, construction activities, or prior discharge of heated nuclear reactor cooling water. The latter disturbance affected stream channel morphology, substrate composition, riparian vegetation, and the quantity and quality of coarse woody debris. The last operating reactor on the Savannah River Site was shut down in 1988, and habitat recovery through secondary succession has occurred in streams that received reactor discharges. Four of the fish sample sites had a reservoir upstream from the site (about 0.5–14 km) and one had a reservoir downstream (about 1 km, Figure 1). The situation was similar for the macroinvertebrate sample sites except that the shortest distance to an upstream reservoir was approximately 2 km rather than 0.5 km.

Field methods

A natural substrate sampling protocol similar to SCDHEC (1998) was used to collect macroinvertebrates from 27 different sites in 12 streams during the summer and fall of 1997, 2000, and 2003 (Figure 1). Sites suffering from possible pollution with toxic chemicals were excluded from analysis. Sites located within the same stream were separated by several kilometer or more, represented ecologically distinct stream reaches, and were considered independent sample sites for the purpose of analysis. Organisms were collected from natural substrates over a 150-m stream reach during three person-hours of sampling effort at each site using a D-frame dip net, kick net, hand sieve, white plastic pan, and fine mesh sampler. The objective was to represent taxonomic composition and diversity with reasonable accuracy at all sites. Taxa were usually identified to genus or species and the level of taxonomic resolution was consistent among sites.

Fish assemblage data were collected from 23 different sites in 11 streams (Figure 1). Most sites were the same as those sampled for macroinvertebrates. A 150-m stream reach (sufficient in total to adequately represent species composition; Paller 1995) was electrofished at each location during the summer and fall of 2003 and 2007. Smaller streams were electrofished with a generator or battery-powered backpack direct current (DC) electrofisher and larger streams were electrofished with two backpack electrofishers or a

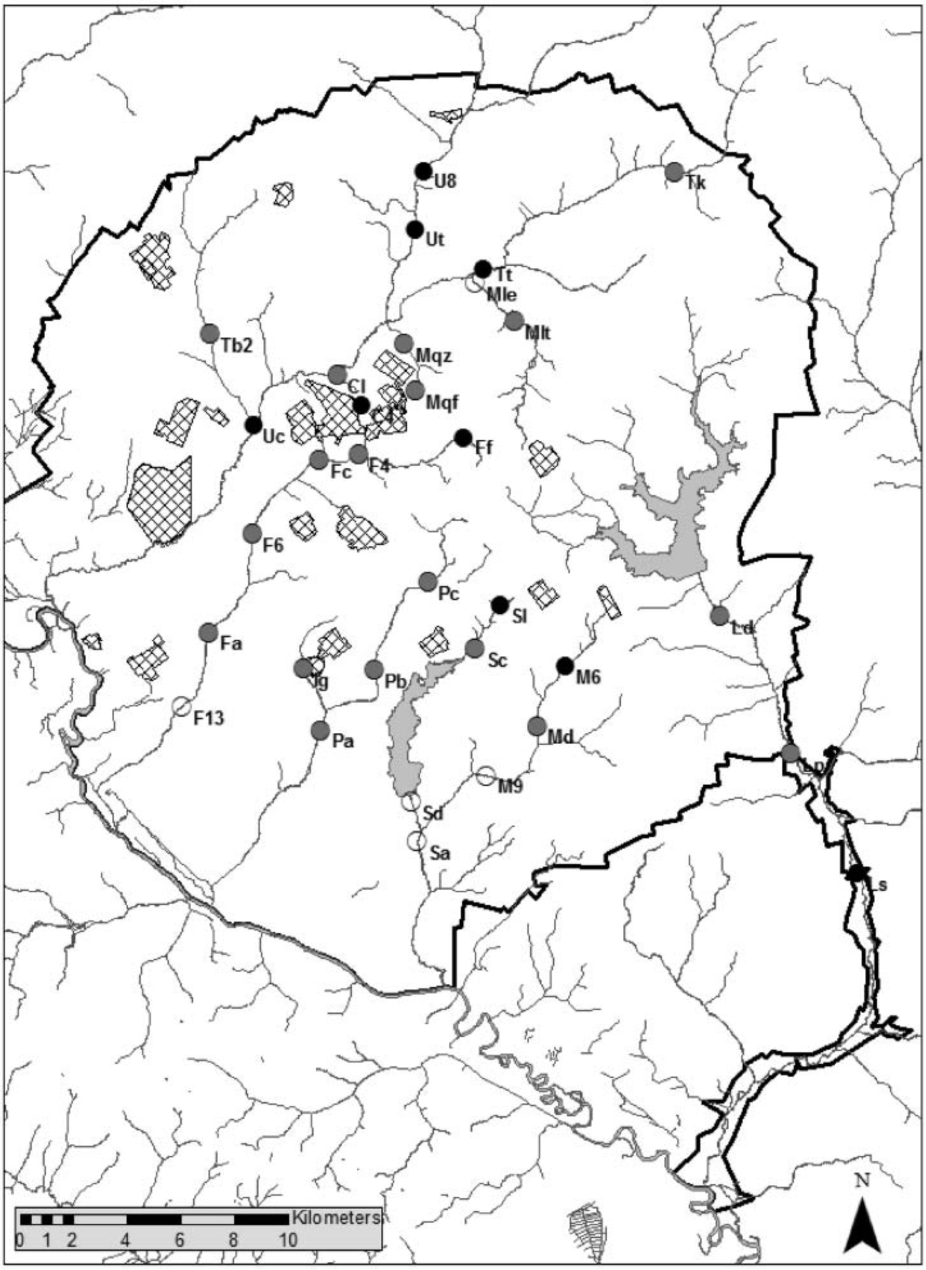

Figure 1. Sample sites for macroinvertebrates and fish. Sites sampled only for fish are represented by open circles, sites sampled only for macroinvetebrates by black circles, and sites sampled for both by gray circles.

boat-mounted DC electrofisher. Using different methods permitted us to maintain a higher and more consistent level of sampling effectiveness (in terms of proportion of the assemblage that was successfully detected) than that would have been possible if a single method had been used at all sites (e.g., a single back pack electrofisher in small as well as large streams). The electrofisher power outputs were adjusted to maximize the number of fish collected without incurring substantial mortality among the collected specimens. A single pass was made through each 50-m segment while moving upstream and all microhabitats were carefully sampled. Fish were identified to species and then released.

A measure of in-stream habitat quality was computed using methods similar to SCDHEC (1998). Variables indicative of anthropogenic disturbance including epifaunal substrate quality, pool substrate quality, pool variability, sediment deposition, channel flow status, channel alteration, channel sinuosity, bank stability, vegetative protection, and riparian vegetation were each rated on a scale of 1 (poor) to 20 (optimal) for each sample site based on visual examination by the same observer. Criteria used for scoring can be found in SCDHEC (1998). The scores for these variables were added to produce a summary measure of in-stream habitat quality for each site. In addition to the preceding variables, stream width at the water surface was measured at each sample site at 7 to 12 evenly spaced transects across the stream perpendicular to the direction of water flow.

Data analysis

A landcover disturbance index was developed as a measure of habitat disturbance at the watershed scale. The index was computed from 2006 United States Geological Survey National Land Cover Data (NLCD) for the catchments (i.e., watersheds or sub-watersheds) associated with each study site. The NLCD data include land cover and land use classifications that are standardized across the USA. The disturbance index included lands characterized in the NLCD as low, medium, and high intensity development plus cultivated, pasture, and bare lands. The area of each land use category within each catchment was individually determined in ArcGIS. The six disturbance categories were then converted to percentages of the total catchment areas and summed to generate the disturbance index for each catchment. Catchment boundaries were delineated from Light Detection and Ranging data.

Six data sets were used in the analysis: fish metric, fish taxa, macroinvertebrate metric, macroinvertebrate taxa, fish environmental, and macroinvertebrate environmental. The taxa data sets consisted of taxa (number of individuals) by sample site matrices – primarily at the genus level for macroinvertebrates and species level for fish. The metric data sets were computed from the taxonomic data sets. Six fish metrics were computed for each sample site: total species richness; number of madtom and darter (*Noturus, Etheostoma,* and *Percina*) species; and percentages of individuals belonging to tolerant, native Cyprinidae, *Lepomis,* and predator species. Tolerant species included bullheads (*Ameiurus* spp.), bowfin (*Amia calva*), carp (*Cyprinus carpio*), mosquitofish (*Gambusia holbrooki*), and golden shiner (*Notemigonus chrysoleucas*). Although not a commonly used metric, number of madtom and darter species was a good indicator of benthic disturbance (such as siltation). Previous work has shown that these metrics accurately reflected anthropogenic disturbances in the streams under study (Paller et al. 1996). With the exception of percentage of tolerant species and percentage of *Lepomis* species, these metrics typically decrease with disturbance. The strongest correlation coefficient (Pearson r) between metrics was 0.73 with most correlations being much lower, indicating that all metrics contributed unique information. Six metrics are fewer than that are used in most similar studies but sufficient to represent species richness, proportional abundance, sensitivity to different types of disturbance, and trophic composition.

There were also six macroinvertebrate metrics: total taxa richness, number of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa, percent clingers (a behavioral group sensitive to sedimentation), percent Ephemeroptera, total number of organisms, and the North Carolina Biotic Index (NCBI, Lenat 1993). The last metric typically increases with disturbance, while the other macroinvertebrate metrics decrease with disturbance. Previous research shows that these metrics are reflective of environmental quality in Savannah River Site streams (Paller et al. 2007) and Atlantic coastal plain streams in general (Maxted et al. 2000). The number of EPT taxa and total number of taxa were strongly correlated ($r = 0.90$) but both were retained in the analysis because of their common use in environmental studies. Correlation coefficients between other macroinvertebrate metrics ranged from 0.22 to 0.74.

Variables in the environmental data matrices included a measurement of in-stream habitat quality and a watershed disturbance index, as previously described, plus stream width and a categorical variable indicating whether a reservoir was present upstream or downstream from each study site. Inclusion of the first two variables permitted us to test our hypothesis that disturbance-related effects, especially at the local in-stream scale, had significant effects on macroinvertebrates and fish. The reservoir variable (1 = presence, 0 = absence) was added to account for potential reservoir-related effects on stream hydrology, habitat connectivity, and the introduction of nonnative (i.e., reservoir) species. The stream width was included because it is an important natural variable that can strongly influence the diversity and taxonomic composition of stream fish and macroinvertebrate communities (Grubaugh et al. 1996; Paller & Specht 2006). An additional categorical variable, presence of a formerly operating reactor upstream from the study site, was initially included in the analysis to account for residual reactor-related impacts that might not be captured by the in-stream habitat quality index but was removed because of its lack of influence on biotic structure.

Multivariate ordination methods were used to identify relationships between biotic communities and the environmental variables and compare the responses of fish and macroinvertebrate assemblages to disturbance. Although the primary emphasis was on metric data, we also ordinated the taxonomic data from which the metric data were derived since it is possible to lose information when multivariate taxonomic data is condensed into metrics and because the derivation of metrics may introduce subjectivity that obfuscates ecological relationships (Norris 1995; Milner & Oswood 2000; Herbst & Silldorff 2006; Lücke & Johnson 2009). We did not include the year in which a site was sampled in the analysis because preliminary cluster analyses indicated an absence of temporal groupings associated with this factor.

We used both direct and indirect ordination methods to ensure that we characterized the unconstrained variability in the biological data sets (indirect ordination) as well as the variability that was directly associated with the environmental variables under study (direct ordination). Indirect methods such as nonmetric multidimensional scaling (NMS) and principal components analysis (PCA) objectively identify patterns in biological data regardless of their source (thereby showing if environmental variables other than those under study were important). Direct methods such as redundancy analysis (RA) and canonical correspondence analysis (CCA) can identify patterns in biological data that are specifically associated with measured environmental variables. Through the use of variance partitioning techniques, it is also possible to assess the amount of unique and shared (i.e., joint) variance in the biological data that is associated with specific environmental variables and statistically test it using Monte Carlo permutation procedures (Jongman et al. 1995; Lepš & Šmilauer 2007).

Biotic data matrices were individually ordinated using NMS based on Sorensen (Bray–Curtis) distances among sites for the taxonomic data and PCA for the metric data. The former method is appropriate for heterogeneous data with many zeroes and the latter for data with more symmetrical distributions and few zeroes. The significance of the NMS ordination axes was determined by a Monte Carlo procedure that compared the stress in the ordinations with the stress in randomized species arrangements (stress measures the correspondence between the original Sorensen distances among sites and the distances among sites indicated by the ordination, McCune & Grace 2002). The significance of the PCA axes was assessed by comparing the observed eigenvalues with eigenvalues generated by a null model (McCune & Grace 2002). Only significant axes are reported. The taxonomic data were log ($x + 1$) transformed prior to analysis to provide a balanced representation of common and rare taxa. Pearson correlation coefficients were calculated between each ordination axis and each environmental variable.

Direct ordination was subsequently used to explicitly assess the influence of the measured environmental variables on each biological data set. Detrended correspondence analyses (DCA) was used in a preliminary analysis to estimate gradient lengths in the biological matrices following Lepš and Šmilauer (2007). Gradient lengths were relatively short for most biological matrices (under 3.0) indicating the appropriateness of RA, but the maximum gradient length for the macroinvertebrate taxa data was 3.60. This denoted an intermediate level of heterogeneity (3.0–4.0, Lepš & Šmilauer 2007) at which both unimodal methods (such as CCA) and linear methods (such as RA) can produce a suitable ordination. Following preliminary comparisons between RA and CCA, we chose RA because it produced stronger correlations with the environmental data and because, theoretically, we expected that most species could be present at most sample sites (i.e., potentially low species turnover). Taxonomic data were centered and log ($x + 1$) transformed, whereas metric data were centered and standardized because the metrics were scaled differently. Rare taxa appearing only once or twice were excluded from the macroinvertebrate taxa data because they contributed insignificant information. For each biological data set (e.g., macroinvertebrate metrics), an initial RA was performed with all environmental variables to extract the total variation explained by the environmental measures. Subsequently, each environmental variable was individually assessed by specifying the other environmental variables as covariables, which identified the unique effect of the variable independent of variance shared with other variables.

Lastly, the Mantel Statistic was computed as a measure of the correlation between the metric and taxonomic matrices describing each biotic group. The standardized Mantel Statistic was computed from similarity matrices derived from the metric and taxonomic data. Computations were conducted with PC-ORD (McCune & Mefford 2011) and Canoco (Ter Braak & Smilauer 2006).

Results

Habitat

Most of the metrics included in the in-stream habitat disturbance index were highly variable among sites, partially as a result of the natural longitudinal changes that occurred along the continuum from first- to fourth-order streams (Figure 2). An exception was width of the intact riparian zone, which received a score of 20 (the maximum) at all sites except two. The lowest scoring metrics were epifaunal substrate, which reflected a general lack of solid substrates with the exception of coarse woody debris and some gravel, and sediment deposition, which reflected the predominance of sand and to a lesser degree silt at the study sites. Both characteristics are to a large degree a consequence of natural factors in the coastal plain streams under study, although sediment deposition also

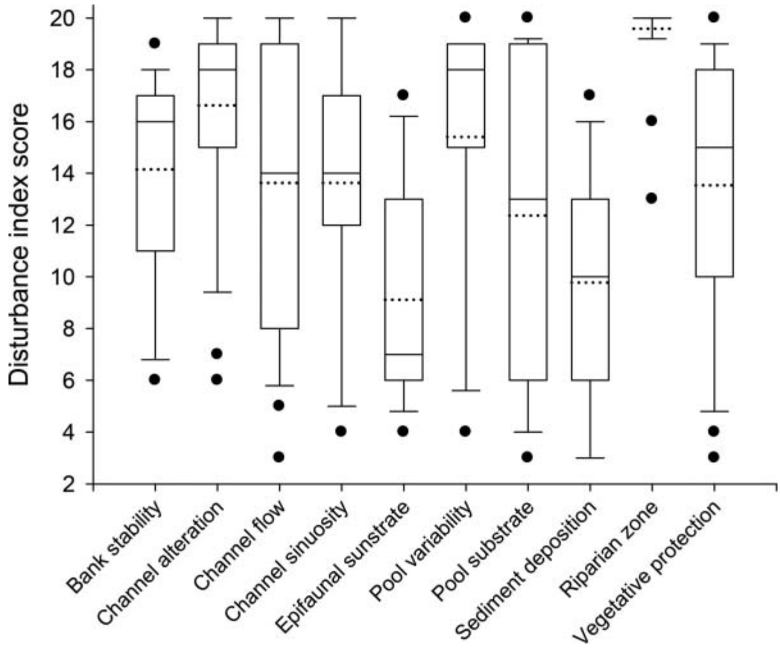

Figure 2. Box plots for in-stream habitat variables used to calculate an in-stream habitat disturbance index (box boundaries = 25th and 75th percentiles, error bars = 90th and 10th percentiles, circles = outliers, lines within boxes = medians [solid] and means [dotted]).

reflected anthropogenic disturbances. The median width of the sample sites at water's edge was 4.9 m (1.5 m–17.1 m). The average percentage of disturbed land in the watersheds under study was 5.8 with a range of 0.2–13.7.

Macroinvertebrates

Over 8100 macroinvertebrates representing 224 taxa were collected from 27 macroinvertebrate sample sites. Among the most abundant genera were *Cheumatopsyche*, *Polypedilum*, *Baetis*, *Palaemonetes, Stenonema, Hydropsyche*, *Tanytarsus*, *Calopteryx, Cricotopus, Simulium*, *Rheotanytarsus*, and *Hyallela*.

The PCA of the macroinvertebrate metric data produced only one significant ($p \leq 0.05$) axis indicating that the sample sites were aligned along a single gradient that was moderately to strongly associated with the six macroinvertebrate metrics ($r = 0.74$ for NCBI and −0.49 to −0.97 for the other metrics) and with the environmental variable in-stream habitat quality ($r = -0.74$, Figure 3(A)). Somewhat weaker associations occurred with stream width and the watershed disturbance index ($r = -0.68$ and 0.44, respectively). Four of the macroinvertebrate sample sites were potentially affected by reservoirs, but these sites appeared unrelated to axis 1 (Figure 3(A)). Pearson correlations were not calculated with the reservoir variable because it was categorical.

The NMS of the macroinvertebrate taxonomic data produced three significant axes (Figures 3(B) and (C)). Stress for this ordination was 12.9% (stress values under 5% indicate strong correspondence with the original matrix; values over 20% indicate weak correspondence and problematic interpretability, McCune & Grace 2002). There were some similarities between the metric and taxonomic ordinations. For example, the sample sites

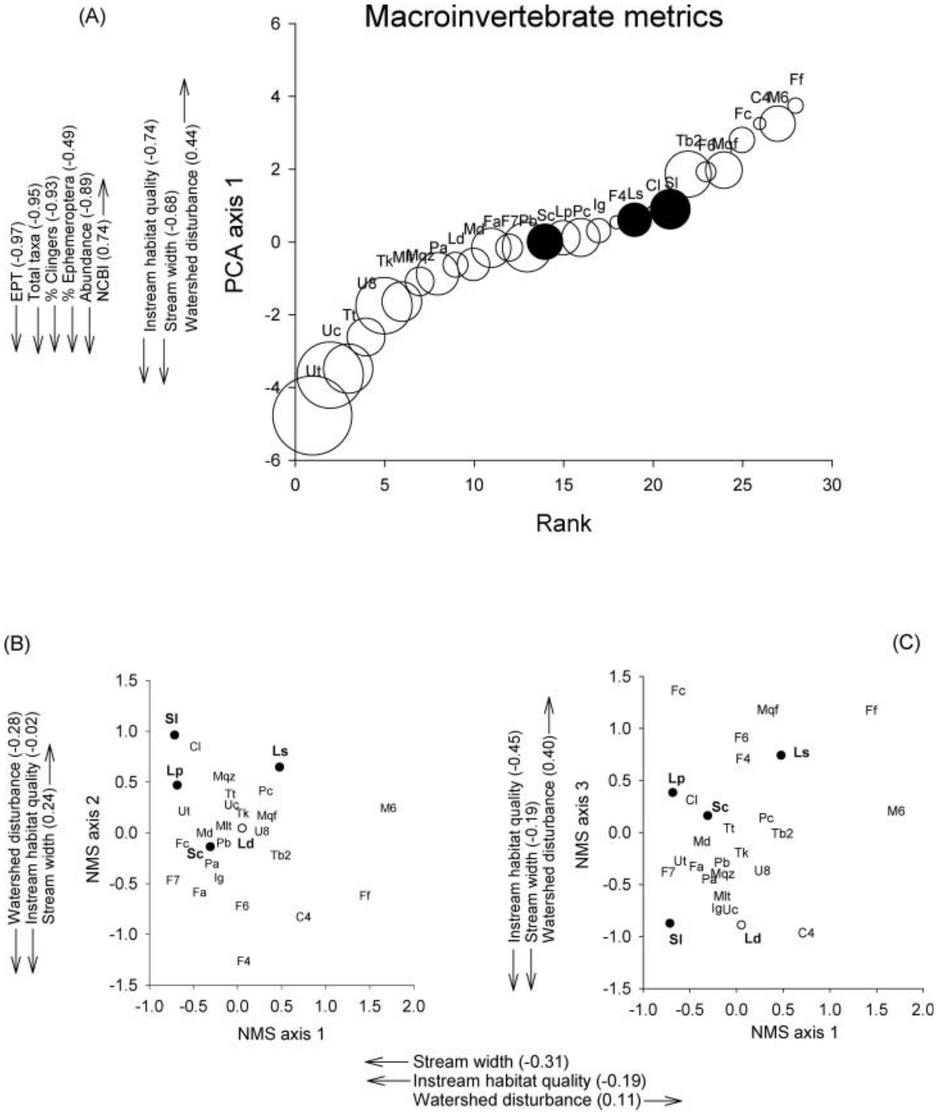

Figure 3. Ordination of sample sites based on macroinvertebrate metric (PCA (A)) and taxonomic data (NMS (B) and (C)). Circle diameters in the metric plot are proportional to total number of taxa. Filled circles represent sites with upstream or downstream reservoirs. Correlations with environmental factors are shown for each axis.

'Ff' and 'M6' were on one end and 'Ut' on the other end of prominent gradients in both analyses; however, other sample sites were patterned differently. Correlations with the environmental variables were weaker in the taxonomic ordination than in the metric ordination: the strongest were with in-stream habitat quality ($r = -0.45$) and watershed disturbance ($r = 0.40$) on axis 3. The standardized Mantel Statistic describing the correlation between the similarity matrices derived from the macroinvertebrate metric and macroinvertebrate taxonomic data sets was 0.56, indicating a substantial but imperfect relationship between the two.

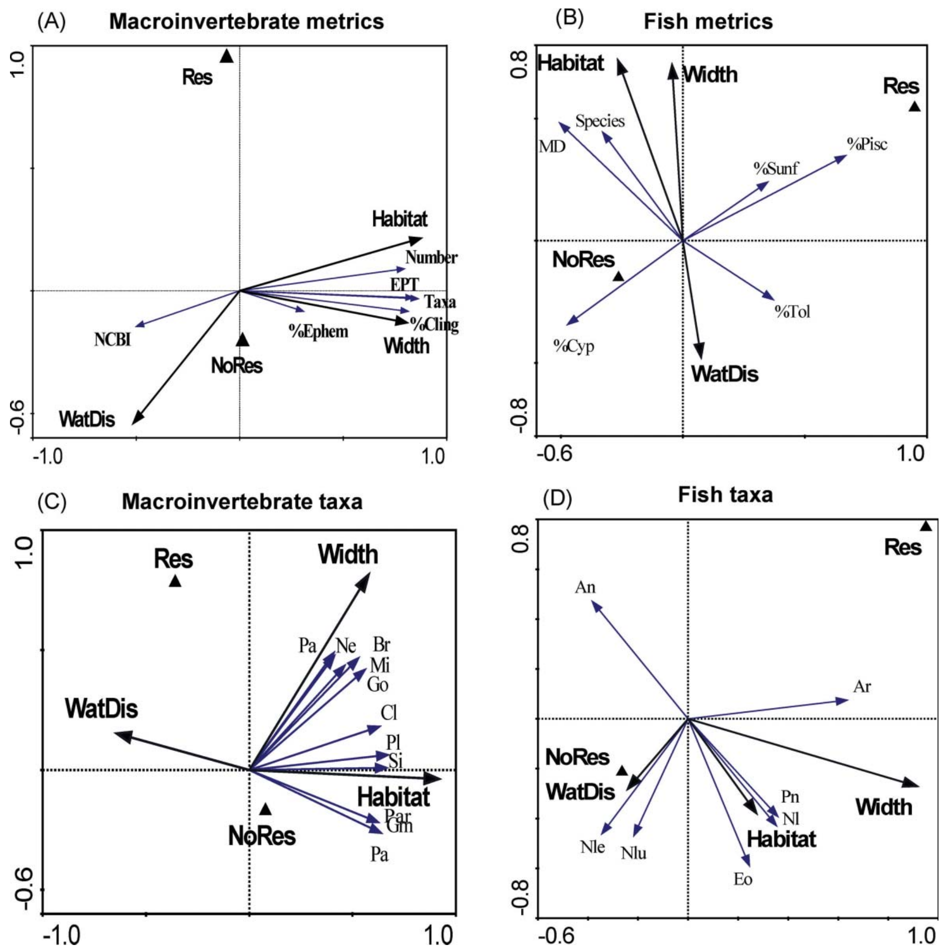

Figure 4. RA of sample sites based on fish and macroinvertebrate data. The metric biplots (A and B) depict metrics and environmental variables. The taxa biplots ((C) and (D)) depict taxa and environmental variables. Arrows indicate directions of increase in these variables. Environmental variables include in-stream habitat (Habitat), stream width (Width), watershed disturbance (WatDis), presence of an upstream or downstream reservoir (Res), and absence of a reservoir (NoRes). Macroinvertebrate assemblage metrics include number of organisms (Number), number of EPT taxa (EPT), number of taxa (Taxa), % clingers (%Cling), % Ephemeroptera (%Ephem), and the NCBI. Fish assemblage metrics include number of species (Species), % sunfish (%Sunf), % piscivores (%Pisc), % tolerant fish (%Tol), number of madtom and darter species (MD) and % native minnows (%Cyp). Taxa abbreviations are explained in the text.

The RA of the macroinvertebrate metric data showed that 52.4% of the variance was explained by the four environmental variables ($p = 0.002$ for all canonical axes). Number of organisms, number of taxa, % clingers, % Ephemeroptera, and number of EPT taxa increased with stream size (width) and in-stream habitat quality (Figure 4(A)). In contrast, the NCBI (which is positively related to disturbance) increased with watershed disturbance.

Variance partitioning techniques were used to assess the unique effect of each of the four environmental variables on the macroinvertebrate metrics after the effects of the other variables were statistically accounted for. The unique effects of stream size and

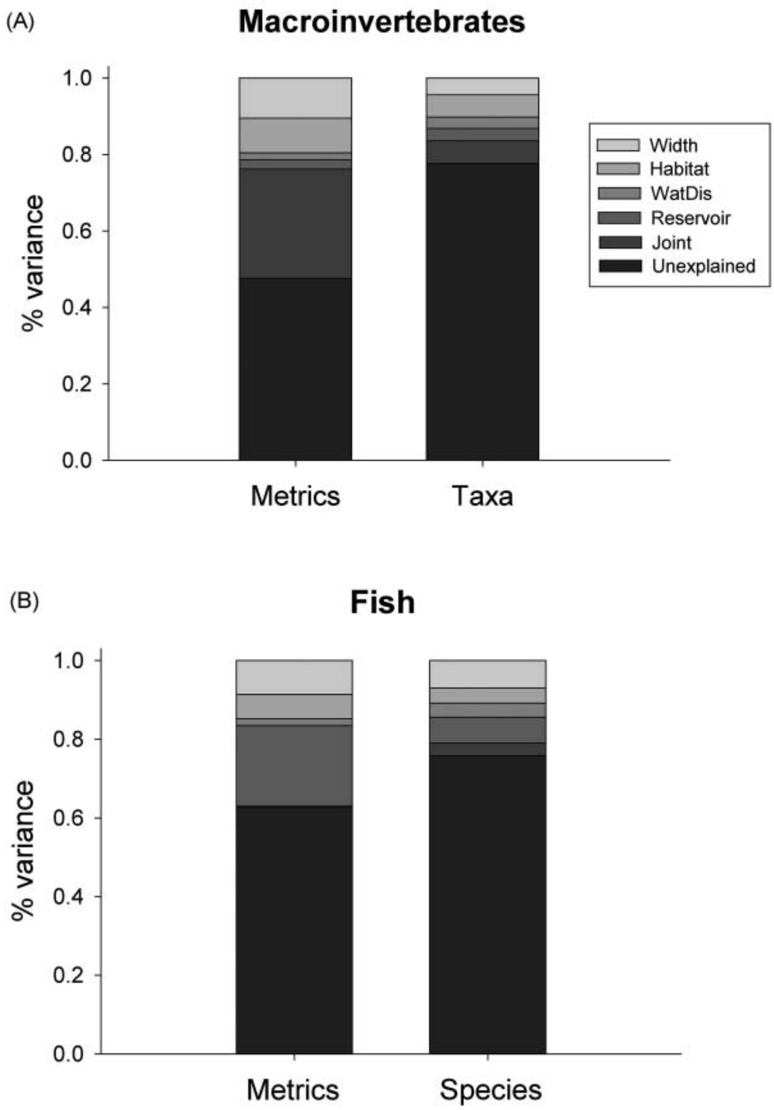

Figure 5. Percentage of variance in macroinvertebrate metrics, macroinvertebrate taxa (A), fish metrics, and fish species (B) explained by stream width, in-stream habitat, watershed disturbance, and presence of an upstream or downstream reservoir. Also shown is joint variance (shared by all variables and not uniquely attributable to any) and variance that was unexplained by the environmental variables.

in-stream habitat disturbance accounted for 10.5% and 9.1% of the metric variance, respectively; both were statistically significant (p = 0.010 and 0.006, respectively, Figure 5(A)). In contrast, neither watershed disturbance nor the presence of a reservoir had a significant unique effect on the macroinvertebrate metrics. The unique variance associated with these variables was only 1.8% and 2.4%, respectively. There was considerable joint (shared) variance among the environmental variables that could not be assigned to specific variables (Figure 5(A)).

The RA of the macroinvertebrate taxonomic data showed that the four environmental variables together explained 22.4% of the variance ($p = 0.004$ for all canonical axes), considerably less than the 52.4% of the variance explained by the environmental variables in the metric analysis (Figure 5(A)). The abundance of most taxa increased with stream width and in-stream habitat quality (Figure 4(C)). Among the more abundant taxa participating in this trend were the chironomids *Parametriocnemus*, *Paralauterborniella*, and *Clinotanypus* (Pa, Par, and Cl in Figure 3) and the trichopterans *Neureclipsis*, *Brachycentrus*, and *Micrasema* (Ne, Br, and Mi). Others included *Gomphus* (Gm), *Gonielmis* (Go), *Paleomonetes* (Pl), and *Sialis* (Si). However, the unique effects of stream width and in-stream habitat accounted for only 4.4% and 5.8%, respectively, of the variance in the taxa data (Figure 4). Only the latter was statistically significant ($p = 0.036$). Watershed disturbance and reservoir presence accounted for 3.0% and 3.2% of the variance in the taxa data; neither was significant.

Fish

Forty-nine fish species representing over 5000 individuals were collected from the 23 fish sample sites. The most abundant species were the yellowfin shiner (*Notropis lutipinnis*), dusky shiner (*Notropis cummingsae*), pirate perch (*Aphredoderus sayanus*), redbreast sunfish (*Lepomis auritus*), spotted sunfish (*Lepomis punctatus*), and bluehead chub (*Nocomis leptocephalus*).

The PCA of the fish metric data produced two significant axes (Figure 6(A)). The first was related to % native minnows ($r = -0.83$), madtom, and darter species ($r = -0.74$), total number of species (−0.58), % piscivorous fish ($r = 0.59$), % sunfishes ($r = 0.49$), and % tolerant fish ($r = 0.82$). The second axis was correlated with total number of species ($r = -0.71$), % sunfishes ($r = -0.69$), and % native minnows (0.47). Axis 1 was weakly correlated with the environmental variables; axis 2 was moderately correlated with in-stream habitat and stream width ($r = -0.50$ and −0.45, respectively). In addition, all five sites that were potentially affected by upstream or downstream reservoirs had relatively low scores on axis 2 (Figure 6(A)).

The fish taxa NMS ordination (stress = 15.3%) was similar to the fish metric ordination in some respects, especially the separation of sites potentially affected by reservoirs (all were predominantly on one end of axis 2, Figure 6(B)). Correlations between the fish taxa ordination axes and the environmental variables were generally low; the strongest was between stream width and axis 2 ($r = 0.47$). Together, the fish metric and taxa ordinations indicated the importance of reservoir-related effects on fish assemblage structure. These affects were associated with greater representation by sunfishes, piscivorous species, and tolerant species and lower numbers of native minnows such as *Semotilus atromaculatus*, *N. leptocephalus*, and *N. lutipinnis*.

Although the fish metric and taxa ordinations shared some similarities, there were also differences. For example, F4 and Fa were on opposite end of axis 1 in the taxa ordination but not the metric ordination. The standardized Mantel statistic describing the correlation between the similarity matrices derived from the fish metric and fish taxonomic data sets was 0.52, which was similar to the correlation between the macroinvertebrate metric and taxonomic matrices.

The RA of the fish metric data indicated that 37% of the variance was explained by the four environmental variables ($p = 0.008$, Figures 4(B) and 5(B)). The metric data were affected by more than one environmental gradient: number of species and number of madtom (*Noturus* spp.) and darter species (*Etheostoma* spp. and *Percina nigrofasciata*)

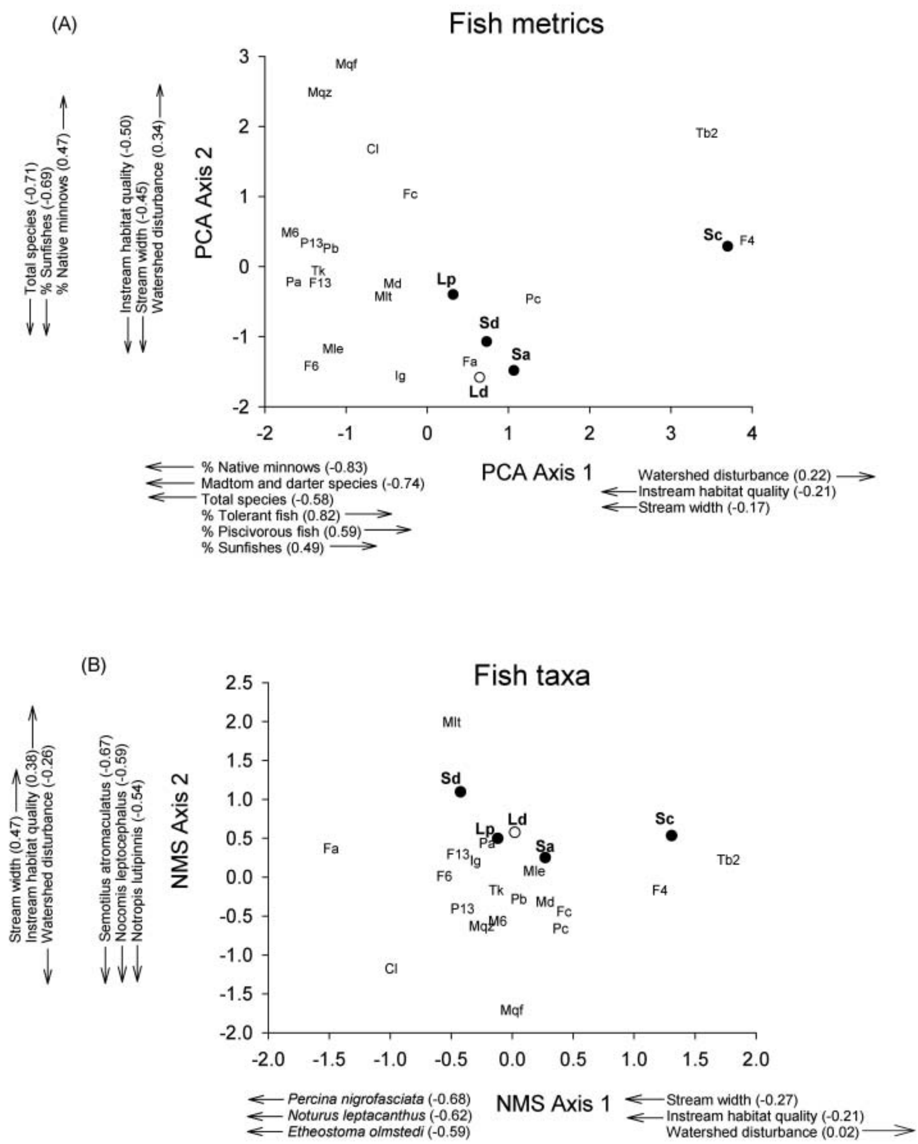

Figure 6. Ordination of sample sites based on fish metric (PCA (A)) and taxonomic data (NMS (B)). Filled circles represent sites with upstream or downstream reservoirs. Correlations with environmental factors are shown for each axis.

increased with stream width and in-stream habitat quality, and % sunfish and % piscivores increased at sites with upstream or downstream reservoirs. The environmental variable with the largest unique effect was reservoir presence (17.3%, $p = 0.008$, Figure 5(B)). The only other variable with a marginally significant unique effect was stream width (7.9%, $p = 0.052$).

The RA of the fish taxa data showed that the environmental variables accounted for 23.7% of the variation in species composition among sites ($p = 0.050$, Figures 4(D) and 5(B)). The darters *P. nigrofasciata* and *Etheostoma olmstedia,* and the madtom *Noturus*

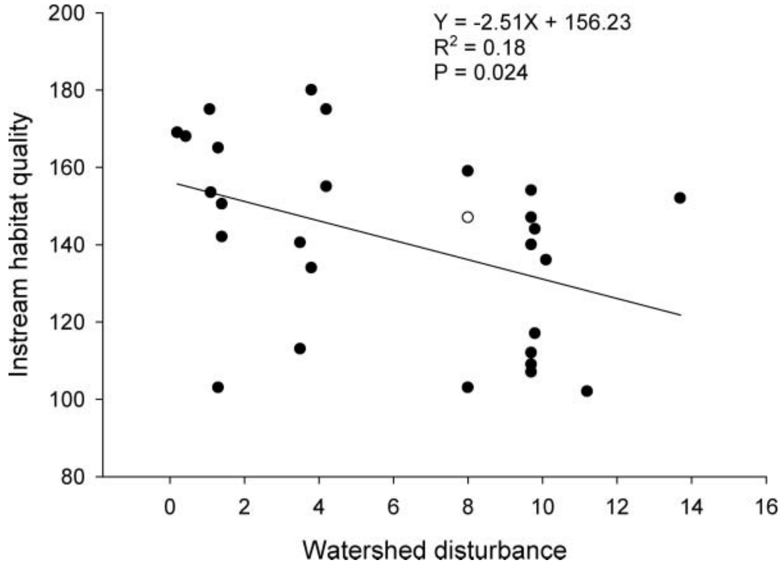

Figure 7. Relationship between watershed disturbance and in-stream habitat quality.

leptacanthus (Pn, Eo, and Nl in Figure 4(D)) were more abundant where in-stream habitat quality was greater and the cyprinids *N. leptocephalus* (Nle) and *N. lutipinnis* (Nlu) were more abundant in smaller streams without reservoirs. However, none of the environmental variables had unique effects that were significant.

Discussion

Not surprisingly, in-stream habitat quality (which was a function of current and legacy disturbances) had significant effects on macroinvertebrates as indicated by both taxonomic and metric data. This finding parallels the results of other studies that highlight the influence of stream habitat on this comparatively sedentary taxonomic group, which is strongly dependent on substrate composition, current velocity, colonizable woody debris, and other local habitat factors. Johnson and Goedkoop (2002) reported that the effect of littoral habitat on macroinvertebrate communities was greater than the effects of environmental factors acting at riparian, catchment, and ecoregion scales, although the latter variables were also important. Other researchers have also reported that macroinvertebrate communities are more strongly affected by reach-scale conditions than conditions at the watershed scale (Richards et al. 1997; Sponseller et al. 2001).

Fish community structure, as indicated by both metric and taxonomic data, was not significantly related to either the in-stream habitat or watershed disturbance measures used in this study. This was probably because of comparatively low levels of disturbance in most Savannah River Site watersheds and a lack of severe in-stream habitat degradation as might be observed in more developed areas. The only significant predictor was the presence of a reservoir downstream or upstream from the sample site. Sample sites with reservoirs had greater numbers of American eels (*Anguilla rostrata*), fishes in centrarchidae (mostly sunfishes, *Lepomis* spp. and largemouth bass, *Micropterus salmoides*), and piscivorous fish (mostly largemouth bass and American eels, Figures 3 and 5). The sample site closest to an upstream reservoir had the most eels, probably because the dam impeded their upstream movement. The presence of largemouth bass was likely due to the dispersal of this species from the reservoirs where they were abundant. Dispersals occurred upstream, as reflected by the immigration of juvenile largemouth bass from a downstream reservoir at one site, and downstream, as a result of the dispersal of largemouth bass in spillway overflow at another (Paller et al. 2006). These results show the importance of reservoirs as sources of invading fishes and disrupters of lotic connectedness (Poff & Hart 2002). Reservoirs can also have downstream effects on macroinvertebrates due to changes in sedimentation, organic matter quantity and quality, water quality and temperature, and other factors (Tiemann et al. 2004; Growns et al. 2009). Such effects were not detected in this study, possibly because the distance from upstream reservoirs was too great for such effects to be measurable using our techniques.

The RA indicated that the amount of variance associated with watershed-scale disturbance was small and statistically nonsignificant. This result differs from those of other studies that show larger effects (Martel et al. 2007), possibly due to the comparatively low levels of watershed disturbance at our sample sites. This reflects the protected status of the Savannah River Site, which has been closed to human habitation since 1950, has limited industrial areas, and has many streams with large, forested buffer zones. The average percentage of disturbed lands in our study was 5.8. This scale of disturbance to upland watersheds may be insufficient to result in statistically detectable effects on aquatic biota. Wang et al. (2003) observed that the influence of watershed-scale variables on fish communities increased with landscape disturbance, and that the relative influence of stream reach-scale variables was greater in undegraded landscapes. This parallels our findings in which more variance in biotic variables was explained by stream reach than watershed scale variables within a landscape that was characterized by only minimal to moderate levels of disturbance. It is also possible that other measures of watershed disturbance may have correlated more strongly with the biotic data than the measure we chose to use, although other measures that we tried (such as the proportion of bare ground, road crossings, and the use of more limited buffer areas around the stream) produced no improvement in our results.

Although not an important predictor in itself, disturbance at the watershed-scale was significantly (although not strongly) related to in-stream habitat quality (Figure 7), indicating that watershed disturbance had an indirect effect on aquatic organisms. Furthermore, the considerable shared variation that could not be uniquely attributed to either in-stream habitat quality or watershed disturbance, likely reflected the interdependence of the two (Figure 4). Similar linkages between reach-scale stream habitat and watershed-scale environmental characteristics have been reported by Johnson and Goedkoop (2002), Wang et al. (2003), and Weigel et al. (2003). It is also important to consider the type of watershed disturbance and its potential for direct effects. Even a small amount of disturbance may have significant effects on stream biota if it results in significant siltation, introduction of contaminants, or changes in hydrology, particularly if sensitive organisms are present. Martel et al. (2007) found that clear cutting a small percentage of forested watersheds in Quebec was sufficient to significantly affect benthic communities, although this was observable only after parsing out the influence of other variables. Severe disturbances, such as clearing of riparian habitats, were uncharacteristic of the watersheds that we studied.

The streams included in this study spanned a comparatively wide size range (first through fourth order) creating the potential for confounding the effects of stream size with disturbance. Stream size-related effects on assemblage composition are a consequence of environmental changes along the stream continuum (Vannote et al. 1980) and the expected patterns of change are often used to adjust bioassessment metrics, especially those related to taxa richness. Such adjustments were not made in this study (although they have been for past bioassessments within the study area, see Paller & Specht 2006). The RA permitted us to assess the unique effects of the disturbance variables on the metrics after accounting for the variance in the metrics that was related to stream size. This approach not only resulted in a potentially more conservative assessment of the relationship between the metrics and the disturbance variables, but also permitted us to examine the independent influence of stream size on the metric and taxonomic data.

Metrics were more strongly related than taxonomic data to measures of disturbance for both macroinvertebrates and fish. There are likely several reasons for this. First, metrics are likely less sensitive than taxon-specific abundances to nondisturbance factors such as sampling problems (e.g., site specific differences in the ability to collect taxa in proportion to their abundance) and natural habitat heterogeneity. Maximum gradient lengths measured by the preliminary DCA were greater for the taxonomic data than for the metric data (3.60 for macroinvertebrate taxa, compared with 0.81 for macroinvertebrate metrics and 2.71 for fish taxa compared with 1.99 for fish metrics) reflecting the greater heterogeneity of the taxonomic data. Variability unrelated to disturbance can lower the proportion of variance explained by disturbance-related variables and reduce their likelihood of attaining statistical significance. Second, taxonomic data are less tractable statistically because of the presence of large numbers of zeroes and departures from normality. However, it is unlikely that this problem fully explains the patterns observed in this study since NMS, a relatively robust and distribution-independent method, also indicated low correlations between the taxonomic data and environmental variables. Last, metrics are explicitly developed and selected for their sensitivity to biotic changes that result from disturbance. Disturbance can remove organisms (Sousa 1984) or act as a filter that excludes taxa sensitive to stress (Poff 1997). Some metrics, such as number of taxa, quantify the loss of organisms with increasing disturbance. Others based on relative abundance, trophic guild composition or pollution tolerance, reflect the exclusion of sensitive taxa and/or increase of tolerant taxa as increasing disturbance alters water quality, habitat suitability, and resource availability. It is not surprising that these measures are effective indicators of ecological integrity.

The main conclusions of this study are the following:

(1) fish and macroinvertebrates responded differently to disturbance. Fish may be particularly sensitive to factors that affect ecosystem connectivity, possibly due to a need to cover relatively large distances to complete life cycles and maintain viable populations. They may also be more susceptible to the effects of invasive reservoir species, particularly predator fishes;
(2) disturbances manifested at the stream reach scale can have a greater effect on macroinvertebrates than disturbances at the watershed scale when disturbed portions of the watershed constitute a minority of the total watershed area. However, disturbances at the watershed-scale are linked to in-stream habitat quality indicating an important indirect effect of the former.

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