

Seasonal variability of landuse impacts on macroinvertebrate assemblages in streams of western Georgia, USA

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Abstract. We examined the influence of land use/land cover (LULC) on macroinvertebrate assemblages and environmental conditions in streams draining 18 small watersheds in the Southern Outer Piedmont ecoregion in Georgia, USA, over a 24-mo period of record. Specifically, we analyzed relationships among LULC categories (i.e., % impervious surface [IS], pasture, silviculture, and deciduous/evergreen forest) and hydrological, physicochemical, and benthic habitat variables, and macroinvertebrate metrics. Macroinvertebrate metrics were related primarily to % IS and % deciduous forest cover, with lowest biotic integrity (species diversity, taxon richness, biological stream condition index) found in high % IS watersheds. Biotic integrity declined with decreasing % forest cover throughout the seasons, and multiple regression models and partial correlation analysis revealed that physicochemical and benthic habitat variables explained more variation in macroinvertebrate metrics throughout the seasons than did hydrological variables at most sites. Based on nonmetric multidimensional scaling, heavily urbanized sites were strongly separated from all other sites in terms of assemblage structure. Total ordination distance among seasonal samples from the same sites increased as % forest cover increased. This pattern might have arisen because urbanized streams had high abundances of a few tolerant, persistent taxa and lacked many ephemeral taxa found in less disturbed systems. The influence of anthropogenic LULC on macroinvertebrate assemblages appears to be consistent throughout the year and reduces seasonal changes in assemblages. LULC-associated differences among assemblages are strongly associated with changes in physicochemistry and benthic habitat conditions that probably are mediated by hydrological alterations associated with altered LULC in the watersheds of this region.

Key words: urbanization, hydrology, physicochemistry, habitat, agriculture, silviculture.

Human activities are responsible for much of the alteration in land use/land cover (LULC) worldwide, and lotic systems and their watersheds are particularly affected by these changes (Hammett 1992, Schnaiberg et al. 2002). LULC in a watershed can influence the overall quality of stream ecosystems by directly altering hydrology, physicochemical conditions, and benthic habitat conditions, which in turn, alters assemblage composition (Bormann et al. 1999, Peterson and Kwak 1999, Clements et al. 2000,

Bledsoe and Watson 2001, Riis and Sand-Jensen 2001). Even slight changes in LULC can affect stream biotic integrity (measured in our study as species diversity, taxon richness, biological stream condition index) dramatically by increasing physiological stress of aquatic organisms, reducing population sizes, and causing alterations in species diversity and other community measures (Lenat and Crawford 1994, Paul and Meyer 2001, Roy et al. 2003, Walters et al. 2003, Allan 2004, Maloney and Feminella 2006).

In the southeastern USA, silviculture, agriculture, and urbanization are common types of land use, and disturbance from each type might apply its own unique suite of pressures on receiving streams (Brown

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et al. 2005). However, urbanization might increase physicochemical stressors and damage receiving waters more than silviculture or agriculture (Allan 2004). Much of the influence of urbanization on streams is considered a direct result of, or mediated by, changes in the hydrologic regime (Paul and Meyer 2001, Allan 2004). Increases in runoff from impervious surfaces and stormwater conveyance can increase magnitude and frequency of storm flows, which can subsequently accelerate nutrient and pollutant transport, alter thermal and decomposition dynamics, erode stream beds, and displace organisms (Jones and Clark 1987, Walsh et al. 2001, Walters et al. 2003, Roy et al. 2005, Chadwick et al. 2006, Brown et al. 2009). The predictable biological effects of watershed disturbance have been identified as a generalized ecosystem distress syndrome or, in urbanized watersheds, the “urban stream syndrome” (sensu Meyer et al. 2005), characterized by reduced biodiversity, altered productivity, and increased abundance of tolerant and exotic species (Rapport et al. 1985, Walsh et al. 2005b).

Effects of LULC on streams often are episodic and become more pronounced with seasonal increases in precipitation and discharge (Weaver and Garman 1994, Helms et al. 2005, Walsh et al. 2005b). Thus, the specific causes of LULC-associated changes in aquatic systems have been elusive because the mechanisms are interrelated and temporally variable (Paul and Meyer 2001, Allan 2004). Stream biological composition usually is seasonally variable (Minshall 1981, Wolda 1988, Bêche et al. 2006). Thus, natural and LULC-associated seasonal changes can be confounded and difficult to disentangle. A better understanding of the temporal influences of LULC on receiving waters at regional scales is essential for effective monitoring, assessment, and management of aquatic resources in streams draining degraded watersheds.

We studied the seasonal variation of the effects of LULC on stream macroinvertebrate assemblages in the Southern Outer Piedmont ecoregion (Griffith et al. 2001) of the USA and examined potential mechanisms associated with observed biological changes. Specifically, we quantified: 1) the influence of LULC on macroinvertebrate assemblages, 2) the relative seasonal influence of putative hydrological, physicochemical, and benthic habitat stressors associated with LULC, and 3) the influence of LULC on seasonality of macroinvertebrate assemblages. Our goal was to develop a temporally integrated, mechanistic understanding of LULC effects on stream biota that could inform attempts to minimize anthropogenic impacts on freshwater systems.

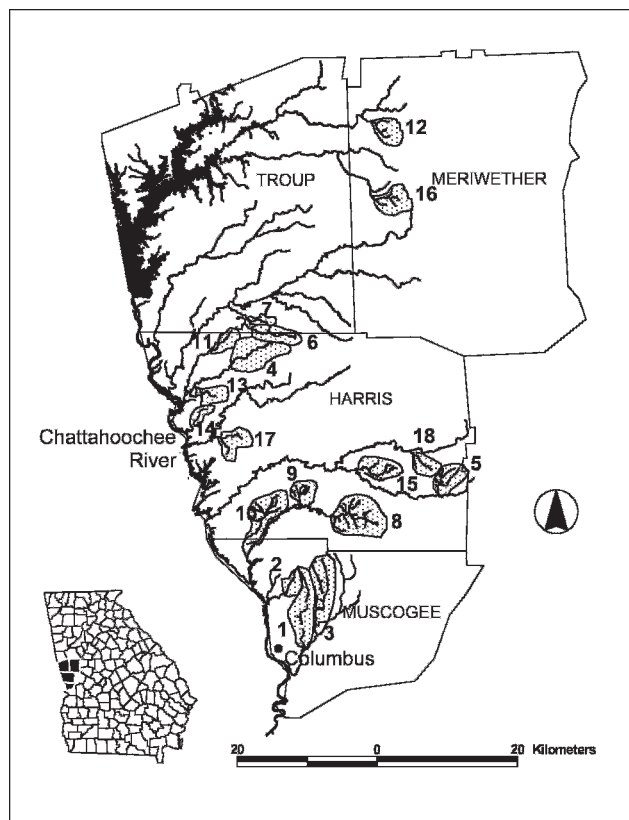


FIG. 1. Study area, which included 18 small watersheds (shaded sections) of the Chattahoochee River Basin in 4 counties in the Southern Outer Piedmont ecoregion in western Georgia, USA. Numbers refer to watersheds and correspond to numbers in Table 1. The city of Columbus is located in western Muscogee County. County names are in capital letters.

Methods

Study area

We studied stream reaches from tributaries of the middle Chattahoochee River, western Georgia, USA, in the Southern Outer Piedmont ecoregion (Griffith et al. 2001). Pasture and forest are being converted rapidly to urbanized areas northeast of Columbus, Georgia, in Muscogee County (Zhang et al. 2008). We sampled 2nd- to 3rd-order streams in 18 watersheds (4–25 km²) from the geologic fall line in the city of Columbus to an area 80 km northeast of the city (Muscogee, Harris, Troup and Meriwether counties; Fig. 1). Study reaches (1/watershed) were ~100 m long and typical of the lower Southern Outer Piedmont, in that they consisted of sandy-bottom channels with run-pool morphometry (Mulholland and Lenat 1992). Our study design enabled us to compare geomorphologically similar streams that differed primarily in watershed-scale LULC and

TABLE 1. Land cover and size characteristics of study watersheds around Columbus, Georgia. Sites denoted by asterisks were sampled only in the 2nd y of the study and were not included in analyses of temporal variation. IS = % impervious surface, P = % pasture, EF = % evergreen forest, DF = % deciduous forest cover in the watershed; ID = watershed identification number in Fig. 1, Trib. = tributary.

ID	Site	Stream	Watershed size (km ²)	IS	P	EF	DF
1	BU1	Lindsey Creek	25.5	40.4	23.3	21.4	12.7
2	RB	Roaring Branch	3.7	30.3	27.1	28.4	11.1
3	BU2	Cooper Creek	24.7	25.1	24.9	30.4	15.9
4	HC2*	House Creek	14.1	1.6	44.0	30.5	22.2
5	MU1	Ossahatchie Creek Trib.	12.0	3.8	36.8	29.2	24.2
6	FS2	Wildcat Creek Trib.	14.5	2.7	35.8	30.7	28.2
7	FS3*	Wildcat Creek Trib.	3.0	2.6	33.9	32.0	29.9
8	SB4	Standing Boy Creek	26.6	3.3	27.7	41.0	22.8
9	SB2	Standing Boy Creek Trib.	6.3	3.4	20.0	37.0	35.5
10	SB1	Schley Creek	20.1	1.9	20.4	38.4	35.1
11	SC	Sand Creek	9.0	1.2	20.9	44.7	28.9
12	MK	Flat Creek Trib.	6.6	2.3	19.8	36.3	38.0
13	HC	House Creek Trib.	6.6	1.3	19.6	47.8	26.8
14	BLN*	Blanton Creek	3.6	1.4	18.7	47.9	28.3
15	MU3	Turntime Branch	10.4	1.9	14.9	41.3	37.2
16	BC	Beech Creek	6.5	2.3	13.3	46.5	34.1
17	MO	Cline's Branch	9.0	1.5	13.0	48.2	33.1
18	MU2	Mulberry Creek Trib.	6.1	1.4	8.8	69.4	13.2

associated variation in streamwater physicochemical conditions.

Land-cover analysis

We determined watershed boundaries and area from US Geological Survey 30-m-resolution digital elevation models and ArcView 3.2a software (Environmental Research Systems Institute, Inc., Redland, California). True-color 1-m-resolution aerial photographs of the study watersheds were taken in March 2003 before leaf emergence. Detailed image-processing methods were presented in Lockaby et al. (2005). Briefly, we manually digitized impervious surfaces (IS) in each watershed from visual cues (e.g., roads, parking lots, and rooftops) and classified other land covers to produce a land-cover classification system similar to the Anderson Scheme (Myeong et al. 2001). For each watershed, we determined % IS, % pasture, % evergreen forest, and % deciduous forest land cover (Table 1). For seasonal analyses, we grouped evergreen and deciduous forest covers to obtain total forest cover, which was used as a single-variable surrogate for general LULC disturbance because IS and pasture were patchily distributed across this landscape (i.e., neither were true gradients individually). We grouped watersheds based on total % forest cover: 1) high forest (>70% total forest cover), medium forest (50–70% total forest cover), and urban

(<50% forest cover). All urban watersheds were in downtown Columbus.

Stream hydrological variables

We quantified stream discharge (Q) from June 2003 to June 2004 with a Mini-Troll[®] pressure-transducer data logger (In-Situ Inc., Ft. Collins, Colorado) installed at the downstream end of each study reach. We set data loggers to measure water depth (stage) every 15 min (0.01-m depth resolution). We then developed stage– Q rating curves to estimate continuous Q (Schoonover et al. 2006). We characterized the following elements of Q from each watershed hydrograph: 1) magnitude (amount of Q for a given interval), 2) frequency (number of occurrences of a given magnitude of Q), and 3) duration (length of time associated with a particular high or low Q event). We calculated 7 hydrologic variables considered important to aquatic biota and useful for separating sites based on LULC (Richter et al. 1996, Poff et al. 1997, Schoonover et al. 2006, Helms et al. 2009). We averaged all values of all hydrological variables from June through September (summer), October through February (winter), and March through May (spring) to obtain seasonal values that corresponded to macroinvertebrate collections. Autumn is not a distinct season in the study region, so we subsumed autumn dates into the summer season for analyses.

Stream physicochemical sampling

We measured several stream-specific physicochemical variables considered important to biological assemblages over the hydrological period of record. We measured stream temperature continuously with HOBO® Temp data loggers (Onset Corp., Pocasset, Massachusetts) placed near the pressure transducers used to measure Q . We measured dissolved O_2 (DO) and streamwater pH seasonally at the same time as macroinvertebrate sampling (see *Habitat and macroinvertebrate sampling* below). We also quantified several nutrient and sediment variables, including total suspended solids (TSS), total dissolved solids (TDS), total P (P), dissolved organic C (DOC), SO_4^{2-} , NH_4^+ , and NO_3^- -N concentrations. We measured each nutrient and sediment variable from streamwater grab samples collected monthly from each watershed (Schoonover and Lockaby 2006). Anions and cations (SO_4^{2-} , NH_4^+ , and NO_3^- -N) were analyzed using a DX-120 Ion Chromatograph (Dionex, Sunnyvale, California). Total P was measured by the molybdate-blue method (Murphy and Riley 1962) and DOC was determined with a Rosemont DC80 organic C analyzer. We averaged values of physicochemical variables for each site within the same seasons described above.

Habitat and macroinvertebrate sampling

We characterized stream habitat and sampled benthic macroinvertebrates in 3 pools and 3 runs per site during September (summer), February (winter), and April or May (spring) 2002 to 2004. We sampled 15 sites in 2002/2003 and the same sites plus 3 additional sites in 2003/2004. We measured mean water depth, wetted width, current velocity (Marsh–McBirney model 2000 flow meter; Marsh–McBirney, Frederick, Maryland) and substrate composition at each run and each pool in each season. We quantified substrate composition by estimating proportional cover of clay, silt, sand, gravel, cobble, wood, detritus, and bedrock in 0.20-increment cover classes in each habitat sampled (modified from Barbour et al. 1999, GADNR 2007). We also quantified mean benthic organic matter (BOM), substrate size, tractive force, (shear stress, T_G ; Gordon et al. 1992), and slope for each stream reach once during the study. We sampled BOM and substrate size in transitional areas between runs and pools to minimize the influence of deposition and scour on our estimates. We quantified BOM as the ash-free dry mass (AFDM) of 9 replicate 2.5×10 -cm benthic core samples. We characterized substrate particle size from 3 benthic samples collected with a 7.62-cm-diameter polyvinyl chloride (PVC) core sampler inserted into the substrate to a depth of

10 cm near where BOM samples were collected. We dried samples and separated particles into 5 size classes: gravel–cobble (>2 mm), very coarse sand (1–2 mm), coarse-to-medium sand (0.25–1 mm), fine sand (0.1–0.25 mm), very fine sand (0.05–0.1mm), and silt/clay (<0.05 mm) to determine median substrate size by mass. We estimated tractive force (T_G) near pressure transducers from the formula

$$T_G = \rho gRS$$

where ρ is the density of water, g is the gravitational acceleration (constant), R is the hydraulic radius, and S is the slope of the energy line (Newbury 1996). Water slope was the average of 3 readings of a surveyor's level and level rod over the 100-m reach.

We sampled macroinvertebrates with a Surber sampler (250- μ m mesh, 0.093- m^2 sampling area). We consolidated multiple Surber collections in each habitat (3 for pools, 4 for runs), to yield 0.27- and 0.36- m^2 composite samples from each pool and run, respectively (1.89 m^2 total area sampled at each study reach per stream and season). We elutriated excess sediment and preserved all samples with 95% EtOH in the field. In the laboratory, we removed all organisms >2 mm with the unaided eye and subsampled the rest at $10\times$ under a dissecting microscope (≥ 300 organisms; Vinson and Hawkins 1996). We counted and measured the length (nearest mm) of macroinvertebrates, identified them to the lowest possible taxonomic level (usually genus or morphospecies) with keys in Merritt and Cummins (1996), Wiggins (1996), and Epler (2001), and assigned them to functional groups (Merritt and Cummins 1996).

We calculated benthic macroinvertebrate metrics selected from standard US Environmental Protection Agency (USEPA) bioassessment protocols (Barbour et al. 1999). We used metrics in 4 broad categories: 1) *taxonomic* metrics included the proportion or taxon richness of taxonomic groups, such as Ephemeroptera, Plecoptera, Trichoptera (EPT) and other putatively sensitive groups; 2) *functional* metrics included the proportion or taxon count of macroinvertebrates in various functional feeding groups (FFGs), habitat-use categories, and tolerance classes; 3) *whole community* variables included diversity (Shannon's H'), taxon richness, total invertebrate biomass (based on published length–mass relationships; Benke et al. 1999), and density; and 4) a *composite* variable, the Georgia Benthic Macroinvertebrate Index, (GA-BMI; GADNR 2007). GA-BMI is an ecoregion-specific multimetric index designed for streams in Georgia, with 6 metrics calculated for the Southern Outer

TABLE 2. Ranges of hydrological variables and Pearson correlation coefficients (r) for statistically significant correlations between annual mean values of hydrological variables and % impervious surface (IS), % pasture (P), % evergreen forest (EF), and % deciduous forest (DF) cover in the watershed. Q = discharge. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Variable	Description	Range	r			
			IS	P	EF	DF
Magnitude						
M	Median Q (L/s)	0.01–0.90		0.49*		
Spate flow frequency						
3×M	No. of times $Q > 3 \times M$	5–116				
5×M	No. of times $Q > 5 \times M$	1–70	0.50*			
7×M	No. of times $Q > 7 \times M$	1–64	0.56*			–0.46*
Spate flow duration						
d3×M	No. of h Q was $> 3 \times M$	36.5–3026				
d5×M	No. of h Q was $> 5 \times M$	6–2518				
d7×M	No. of h Q was $> 7 \times M$	1.5–2412				

Piedmont. Total scores between 100 and 84 indicate very good, 56 to 83 indicate good, 32 to 55 indicate fair, 17 to 31 indicate poor, and <17 indicate very poor ratings (GADNR 2007).

Statistical analyses

We used Pearson correlation analyses (Zar 1999) to explore relationships of annual hydrological, habitat, chemical, and macroinvertebrate variables to LULC categories to determine basic landscape-scale trends in the overall data set. We correlated seasonal means of the whole-community metrics with % total forest cover to investigate changes in the macroinvertebrate community over time. We used stepwise multiple regression ($p = 0.05$ to enter and exit the model) followed by partial correlation analysis to determine the environmental variables with the highest explanatory power for seasonal values of macroinvertebrate metrics. We avoided multicollinearity by including in final models only variables with variance inflation factors (VIF) <10 (Myers 1990).

We used seasonal relative abundances of macroinvertebrates (restricted to those identified to genus) and excluded rare taxa (those occurring in only 1 site) in ordination and indicator value analyses. Each site was represented 6 times in the resulting ordination (summer, winter, and spring for 2 y). We used nonmetric multidimensional scaling (NMDS) of a species × site matrix (Sørensen distance) to describe overall variation in macroinvertebrate assemblages among the sites that were sampled for 2 y ($n = 15$). We based NMDS on 40 runs with real data, 50 runs of randomized data, and 400 maximum iterations using a random starting configuration (McCune and Grace 2002). We followed NMDS by indicator species analysis (ISA; Dufrêne and

Legendre 1997) based on the NMDS site × species matrix to identify the species that were most closely associated with each watershed LULC category. ISA produces indicator values for each taxon in each a priori group by combining taxon abundances and regularity of occurrence in a particular group. We used Monte Carlo randomization (1000 permutations) to test indicator values (Dufrêne and Legendre 1997, McCune and Grace 2002).

We used all axes of the NMDS ordination to calculate seasonality as the total Euclidean distance between sequential samples at each site (i.e., [summer₁ to winter₁] + [winter₁ to spring₁] + [spring₁ to summer₂] + [summer₂ to winter₂] + [winter₂ to spring₂]). We used this distance as a measure of site-specific temporal variation, with higher Euclidean distance values indicating larger temporal differences (Brown 2003). We regressed total Euclidean distance against LULC and correlated Euclidean distance with macroinvertebrate metrics.

We used SAS (version 8.2; SAS Institute Inc., Cary, North Carolina) for all correlation and regression analyses, PC-ORD (version 4; MjM Software Design, Glenden Beach, Oregon) for NMDS and ISA, and R (version 2.7.2; R Foundation for Statistical Computing, Vienna, Austria) for determining Euclidean distances.

Results

Relationships between environmental variables and LULC categories

Three of 7 hydrological variables were significantly correlated with LULC categories (Table 2). Spate flow frequency (number of times Q was > 3 , 5, or $7 \times$ median Q [M]) increased with % IS and decreased with % deciduous forest, as evidenced by the positive

TABLE 3. Ranges of physicochemical variables and Pearson correlation coefficients (r) for statistically significant correlations between annual mean values of physicochemical variables and % impervious surface (IS), % pasture (P), % evergreen forest (EF), and % deciduous forest (DF) cover in the watershed. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Variable	Description	Range	r			
			IS	P	EF	DF
Temp	Mean streamwater temperature (°C)	13.3–15.8	0.83***			–0.61***
DO	Mean streamwater dissolved O ₂ (mg/L)	8.6–14.5	–0.50*			0.55*
pH	Mean streamwater pH	5.7–6.9				
TSS	Mean total suspended solids concentration (mg/L)	2.1–8.1		0.54*		
TDS	Mean total dissolved solids concentration (mg/L)	19.95–58.63	0.58*			
NO ₃ [–]	Mean monthly NO ₃ [–] concentration (mg/L)	0.14–4.45		0.75***	–0.54*	
SO ₄ ^{2–}	Mean monthly SO ₄ ^{2–} concentration (mg/L)	0.53–9.19	0.82***			–0.48*
NH ₄ ⁺	Mean monthly NH ₄ ⁺ concentration (mg/L)	0–0.33				–0.69**
P	Mean total P concentration (mg/L)	0.05–0.12				
DOC	Mean monthly dissolved organic C concentration (mg/L)	1.59–8.55				

relationships between % IS and 5×M and 7×M and negative relationship between % deciduous forest and 7×M. M increased with % pasture, but annual means for spate flow duration (number of h Q was >3, 5, or 7×M) were not significantly correlated with LULC categories.

Several physicochemical conditions also were correlated with LULC categories (Table 3). Water temperature increased and DO concentration decreased with increasing % IS, whereas water temperature decreased and DO concentrations increased with increasing % deciduous forest. TSS increased with % pasture, whereas TDS increased with % IS. NO₃[–]-N concentrations increased with increasing % pasture and decreased with increasing % evergreen forest, whereas SO₄^{2–} and NH₄⁺ concentrations decreased with increasing % deciduous forest, and SO₄^{2–} increased with % IS.

Several stream habitat variables were correlated with LULC categories (Table 4). Substrate size increased with % IS. The proportions of gravel and bedrock increased with % IS, and the proportion of gravel decreased with increasing % pasture. The proportions of wood increased, whereas the proportion of bedrock decreased, with increasing % evergreen forest. The proportions of detritus and wood decreased with increasing % IS.

Variation in macroinvertebrate assemblages among LULC categories and seasons

A total of 184 unique taxa in 52 families were collected. Chironomidae (Diptera), Hydropsychidae (Trichoptera), Tubificidae (Haplotaxida), and Simuliidae (Diptera) were the 4 most common groups. Gatherers and filterers generally were the most abundant FFGs, whereas scrapers were the least abundant FFG (Table 5). Shredders had the highest

single occurrence (87.6% of total abundance), but were undetected in winter and spring samples in all streams. Numerical dominance of FFGs varied by season; shredders and filterers were dominant in summer, gatherers in winter, and filterers and gatherers in spring (Table 5). Clingers, filterers, gatherers, and predators occurred at all sites but not in all seasons.

Major taxonomic differences were evident along LULC categories (Table 6). Annual means of several macroinvertebrate variables were related to % IS or % deciduous forest. GA-BMI, H' , EPT richness, Diptera richness, and Coleoptera richness, and total taxon richness all decreased with increasing % IS and increased with increasing % deciduous forest. Total invertebrate biomass, mean % tolerant organisms, and mean % Oligochaeta increased with increasing % IS and decreased with increasing % deciduous forest (Table 6). Percent filterers and % Trichoptera increased with increasing % IS, whereas % Plecoptera decreased with increasing % pasture.

The GA-BMI, taxon richness, and H' increased with % forest in all seasons (Fig. 2A–I). Density and biomass were not significantly related to LULC categories. In summer, GA-BMI scores, taxon richness, and H' were low in 1 heavily forested watershed (MU2) (Fig. 2 A–C). This watershed was clear-cut 1 to 2 y before our study, so much of the forest was very young. When we omitted this outlier watershed, the percentage of variation explained by LULC categories increased markedly for most metrics (Fig. 2 A–I). In all seasons, correlations among composite macroinvertebrate metrics, particularly GA-BMI and taxon richness, and % forest were strong.

Environmental relationships with macroinvertebrates

Multiple regressions and partial correlations revealed that most macroinvertebrate metrics were

TABLE 4. Ranges of habitat variables and Pearson correlation coefficients (r) for statistically significant correlations between annual mean values of physicochemical variables and % impervious surface (IS), % pasture (P), % evergreen forest (EF), and % deciduous forest (DF) cover in the watershed. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Variable	Description	Range	r			
			IS	P	EF	DF
Size ^a	Watershed size (km ²)	3.0–26.6				
Slope ^a	Water slope of sampled reach (%)	0.03–0.68				
Substrate ^a	Median substrate size (cm)	0.5–1.8	0.52*			
T _C ^a	Tractive force (N/m ²)	2.7–73.9				
BOM ^a	Mean benthic organic matter (g)	0.3–1.2			0.51*	
Depth	Mean water depth (cm)	7.9–26.9	0.69**		–0.60**	–0.49**
Width	Mean wetted channel width (m)	1.6–5.9	0.64**		–0.59*	–0.62**
Flow	Mean current velocity (m/s)	0.07–0.38				
Clay	Proportion clay	0–0.07				
Silt	Proportion silt	0–0.18				
Sand	Proportion sand	0.20–1.00				
Gravel	Proportion gravel	0–0.52	0.46*	–0.57*		
Cobble	Proportion cobble	0–0.43				
Wood	Proportion wood	0–0.22	–0.52*		0.47*	
Detritus	Proportion detritus	0–0.17	–0.51*			
Bedrock	Proportion bedrock	0–0.22	0.49*		–0.56*	

^a Variable was not sampled seasonally.

TABLE 5. Seasonal ($n = 15$ sites sampled twice + 3 sites sampled once = 33) and annual ($n = 18$ sites) means for selected macroinvertebrate metrics. Ranges are given for seasonal means at each site ($n = 99$). EPT = Ephemeroptera, Plecoptera, Trichoptera, H' = Shannon diversity, GA-BMI = Georgia Benthic Macroinvertebrate Index.

Metric	Summer	Winter	Spring	Annual	Range
Taxonomic					
EPT	6.9	7.6	7.3	7.3	1.0–17.0
% Ephemeroptera	9.0	1.6	2.8	4.4	0.0–27.8
% Plecoptera ^a	0.3	8.9	1.5	3.5	0.0–32.8
% Trichoptera	15.6	1.0	7.2	7.9	0.0–55.8
Diptera	18.2	18.2	21.1	19.2	7.0–31.0
% Chironomidae	65.1	70.0	72.9	69.5	22.9–98.8
Coleoptera ^a	2.2	70.0	72.9	69.5	22.9–98.8
% Oligochaeta ^a	2.1	8.8	10.0	7.1	0.0–67.6
Functional					
% shredders ^a	38.4	0.0	0.0	12.3	0.0–87.6
% scrapers ^a	3.5	0.9	1.2	1.9	0.0–12.3
% filterers	25.5	10.8	19.8	18.7	0.7–64.1
% gatherers	17.5	20.6	18	18.7	0.3–41.6
% predators	10.3	11.0	10.7	10.7	0.3–41.8
% clingers	4.7	0.5	1.8	2.3	0.0–15.3
% swimmers ^a	1.4	0.9	1.7	1.3	0.0–3
% tolerant	3.1	1.8	10	5.1	0.0–48.6
Community					
H'	2.1	1.9	2.1	2.0	0.8–2.9
Taxon richness	34.1	33.3	38.8	35.5	14–64
Biomass (g/m ²)	16.5	26.9	43.5	32.9	6.9–101.6
Density (no./m ²)	12,510	21,307	19,998	15,119	2504–68,429
Composite					
GA-BMI	49.4	30.2	30	36.3	3–75

^a Metric included in GA-BMI

TABLE 6. Ranges (based on annual means) of macroinvertebrate assemblage variables and Pearson correlation coefficients (r) for statistically significant correlations between annual mean values of macroinvertebrate variables and % impervious surface (IS), % pasture (P), % evergreen forest (EF), and % deciduous forest (DF) cover in the watershed; GA-BMI = Georgia Benthic Macroinvertebrate Index; EPT = Ephemeroptera, Plecoptera, Trichoptera; H' = Shannon diversity. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Variable	Range	r			
		IS	P	EF	DF
GA-BMI	3–75	−0.70**			0.62**
H'	0.8–2.9	−0.51*			0.69**
Taxon richness	14–64	−0.74***			0.79***
Biomass	6.9–101.6	0.61**			−0.49*
% filterers	0.7–64.1	0.55*			
% tolerant	0–48.6	0.89***			−0.76***
EPT richness	1–17	−.64**			0.71**
% Plecoptera	0–32.8		−0.47*		
% Trichoptera	0–55.8	0.52*			
Diptera richness	7–31	−0.76***			0.80***
Coleoptera richness	22.9–98.8	−0.59**			0.64**
% Oligochaeta	0–67.6	0.91***			−0.74***

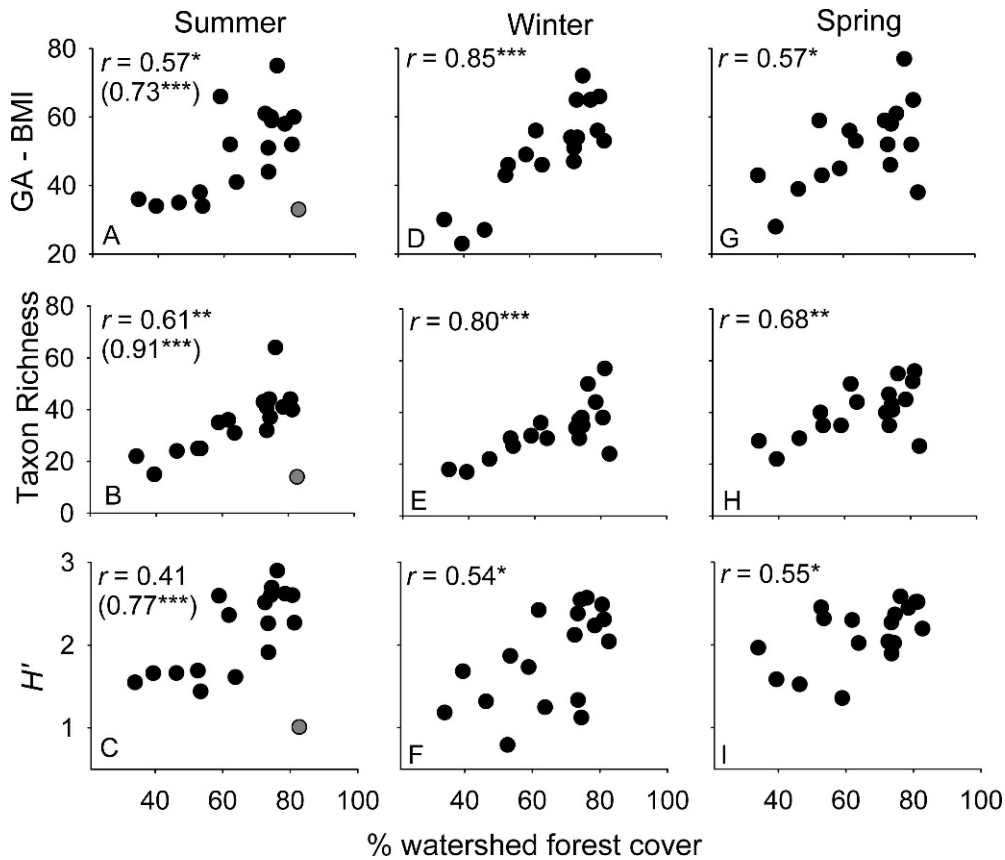


FIG. 2. Scatterplots for correlations between the Georgia Benthic Macroinvertebrate Index (GA-BMI) (A, D, G), taxon richness (B, E, H), and Shannon diversity (H') (C, F, I) in summer (A, B, C), winter (D, E, F), and spring (G, H, I) % watershed forest cover (deciduous + evergreen). The grey points in each panel corresponds to site MU2, which was considered an outlier. The r -values for correlations without this outlier are in parentheses. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

TABLE 7. Best models, partial correlation coefficients for each variable (r), and coefficient of determination (R^2_{adj}) for macroinvertebrate metrics of samples collected during summer, winter, and spring. See Tables 2, 3, and 4 for explanations and abbreviations for variables. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. – indicates no significant predictor was found.

Metric	Summer	r	R^2_{adj}	Winter	r	R^2_{adj}	Spring	r	R^2_{adj}
Taxon richness	TDS	–0.73	0.54**	TDS	–0.89	0.82**	DO	0.89	0.80***
	Temp	–0.58		Detritus	0.82		Silt	0.73	
H'	TDS	–0.63	0.52**	Silt	0.68	0.53**	Wood	–0.58	
	DO	–0.58		Temp	0.65		–	–	–
Density	Temp	–	0.38**	–	–	–	Sand	–0.67	0.59***
Biomass	d3×M	–0.63	0.40**	–	–	–	d3×M	0.53	
	5×M	0.53		–	–	–	Sand	–	0.25*
GA-BMI	TDS	–	0.29*	TDS	–0.91	0.84***	DO	0.68	0.55**
	–	–	–	d7×M	0.71		d7×M	0.56	
	–	–	–	Detritus	–0.67		Detritus	0.39	

better explained by physicochemical and habitat variables than by hydrological variables. With the exception of macroinvertebrate biomass in the summer, the best predictor of all metrics, based on partial correlation coefficients, was a physicochemical or habitat variable (Table 7). In summer, TDS, mean stream temperature, and DO concentrations best predicted taxon richness, H' , density, and GA-BMI, whereas spate flow duration > 3×M and spate flow frequency > 5×M best predicted biomass. In winter, TDS and proportion of detritus best explained taxon richness; TDS, spate flow duration > 7×M, and proportion of detritus best explained GA-BMI; and proportion of silt and mean water temperature best described H' . In spring, DO and proportions of silt and wood best explained taxon richness, and proportions of sand and spate flow duration best described density. In spring, proportion of sand best described biomass, whereas proportion of detritus, DO, and spate flow duration 7×M best described GA-BMI (Table 7). No environmental variable predicted density or biomass in winter or H' in spring.

Seasonality in macroinvertebrate assemblages

Twenty-five taxa were significant LULC indicators. Eighteen taxa were predominantly associated with high-forest watersheds. *Hexatoma* was an indicator for medium-forest watersheds, *Simulium* was an indicator for high- and medium-forest watersheds, and 5 taxa were indicators for urban watersheds (Table 8). Many high-forest indicators were EPT taxa (e.g., *Ephemerella*) or pollution-sensitive Coleoptera (e.g., *Optioservus*), whereas urban indicators generally were pollution-tolerant taxa (e.g., *Physella*).

NMDS axes 1, 2, and 3 described 82.5% of the total variation in the macroinvertebrate assemblages over the 2-y study (29.3, 20.1, and 33.2%, respectively; stress = 15.7, instability = 0.00001, iterations = 106; Fig. 3A–C). Some seasonal grouping of sites was found, generally along axis 2 (Fig. 3B). High- and medium-forest watersheds generally were not separated in the ordination, but urban streams often grouped together, particularly in the plots of axis 1 vs 3 and 2 vs 3 (Fig. 3B, C).

Total Euclidean (seasonal) distances for individual sites in the NMDS ordination ranged from 3.71 in heavily urbanized BU1 to 6.89 in heavily forested SB1. Sites in urban watersheds were less temporally variable than were sites in other LULC categories, particularly on axes 1 and 3 (Fig. 4A–C). Seasonal distance increased significantly with increasing % forest ($R^2 = 0.60$, $p = 0.001$; Fig. 5A) and was correlated with taxon richness ($r = 0.676$, $p = 0.006$), H' ($r = 0.663$, $p = 0.007$), and GA-BMI ($r = 0.639$, $p = 0.010$; Fig. 5B–D).

Discussion

The reality of the landscape mosaic

Environmental factors that shape benthic macroinvertebrate distributions in streams are numerous, often interactive, and frequently associated with landscape disturbance (Allan 2004). LULC is particularly influential on macroinvertebrate assemblage structure, and its effects persist across seasons (Lenat and Crawford 1994, Roy et al. 2003, Maloney et al. 2008, our study). Urbanization is one of the most pervasive and damaging types of landscape disturbance on aquatic systems (Paul and Meyer 2001). In our study, streams in heavily urbanized watersheds

TABLE 8. Significant indicator values (as % of perfect indication), functional feeding group (FFG), and tolerance value (tolerance) of each genera for each land use/land cover (LULC) category. SH = shredder, SC = scraper, GC = collector/gatherer, PR = predator, CF = collector/filterer, FC = filterer/collector, OM = omnivore.

Order:Family	Genus	FFG	Tolerance	LULC group		
				High forest	Medium forest	Urban
Coleoptera						
Elmidae	<i>Anchytarsus</i>	SH	3.8	25	5	0
Elmidae	<i>Optioservus</i>	SC	2.7	35	8	0
Diptera						
Chironomidae	<i>Corynoneura</i>	GC	6.2	43	25	11
Chironomidae	<i>Nilotanypus</i>	PR	4	35	4	0
Chironomidae	<i>Parametriocnemus</i>	GC	3.7	45	23	10
Chironomidae	<i>Pseudorthocladius</i>	GC	0	43	10	0
Chironomidae	<i>Thienemannimyia</i>	PR	6	28	23	48
Empididae	<i>Hemerodromia</i>	PR	6	27	1	3
Simuliidae	<i>Simulium</i>	FC	4.4	44	44	0
Tabanidae	<i>Tabanus</i>	PR	9.7	20	1	0
Tipulidae	<i>Hexatoma</i>	PR	4.7	37	46	0
Ephemeroptera						
Baetidae	<i>Centroptilium</i>	GC	6.3	31	2	0
Ephemerellidae	<i>Ephemerella</i>	OM	2.8	22	1	0
Heptageniidae	<i>Stenonema</i>	SC	3.4	45	26	0
Isonychidae	<i>Isonychia</i>	FC	3.8	20	0	0
Isopoda						
Asellidae	<i>Lirceus</i>	GC	7.7	27	10	0
Odonata						
Coenagrionidae	<i>Argia</i>	PR	6	0	0	33
Corduliidae	<i>Macromia</i>	PR	6.7	17	0	0
Gomphidae	<i>Gomphus</i>	PR	6.2	34	24	0
Plecoptera						
Perlidae	<i>Acroneuria</i>	PR	2.2	33	13	0
Perlodidae	<i>Isoperla</i>	PR	2.3	32	7	0
Pulmonata						
Physidae	<i>Physella</i>	SC	9.1	0	1	55
Trichoptera						
Hydropsychidae	<i>Cheumatopsyche</i>	FC	6.6	20	11	63
Philopotamidae	<i>Chimarra</i>	FC	2.8	30	1	0
Veneroida						
Corbiculidae	<i>Corbicula</i>	FC	6.3	3	14	63

had consistently lower biotic integrity and invertebrate assemblages that were generally different from assemblages in other watersheds. These results suggest an alternative urban stable state or dynamic regime (Scheffer and Carpenter 2003). Urban sites were characterized by increased proportions of a suite of tolerant taxa (e.g., physid snails, *Corbicula*, hydropsychid caddisflies, oligochaetes) and lower abundances of many otherwise-common macroinvertebrate taxa. This pattern probably was a function of increased spate flow frequencies and associated inputs from overland flow, elevated water temperature, and decreased DO and benthic habitat, which

together comprise part of the urban stream syndrome (Walsh et al. 2005b).

Outside urban or residential areas, the western Georgia landscape is a mosaic of LULC that includes agriculture, silviculture, and deciduous forest. Historically, agriculture in this area was mostly cotton cultivation, but has shifted to pasture, which is less damaging than intensive cultivation to receiving waters (Strayer et al. 2003). Disturbance from timber harvest is often less intense than that from agriculture (Fortino et al. 2004), but stream biotic integrity is strongly affected by timber harvest in low-gradient streams of the Southern Outer Piedmont, and the

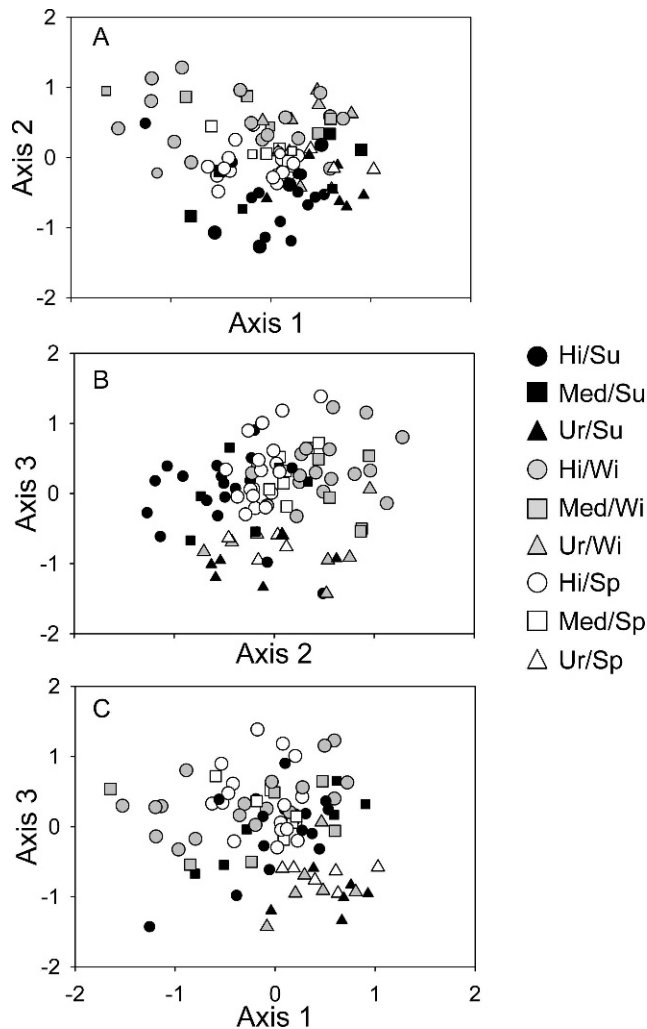


FIG. 3. Nonmetric multidimensional scaling ordination (NMDS) plots of sites in species space based on macroinvertebrate relative abundance on NMDS axes 1 vs 2 (A), 2 vs 3 (B), and 1 vs 3 (C). Symbols represent sites, shapes indicate land use/land cover (LULC) category (Hi = high forest, Med = medium forest, Ur = urban), and fills indicate season (Su = summer, Wi = winter, Sp = spring). Axes are scaled proportionate to the longest axis (% of maximum) and are consistent among panels. Axis 1 explained 29.3%, axis 2 explained 20.1%, and axis 3 explained 33.2% of the total variation in assemblage composition among sites.

magnitude of this effect depends upon the type and timing of harvest (Goodman et al. 2006).

In our study, biotic integrity of stream assemblages increased with increasing % forest. Watersheds with medium forest cover (50–70%) generally had the highest % pasture (28–44%), and sites in these watersheds generally had intermediate levels of biotic integrity. Sites in watersheds with high forest cover, many of which contained extensive pine plantations, had the highest biotic integrity. The only recent clear-

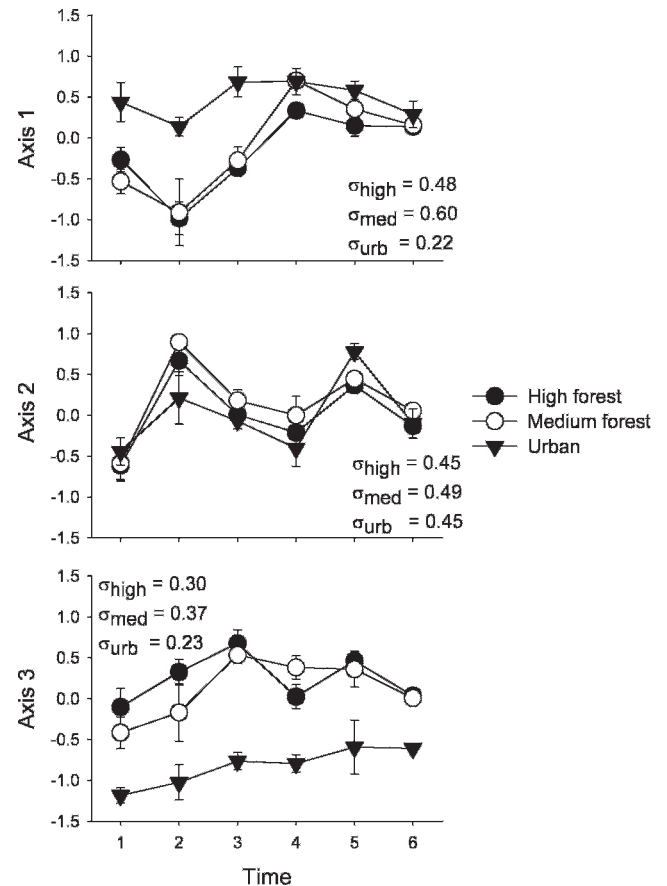


FIG. 4. Macroinvertebrate nonmetric multidimensional scaling (NMDS) scores as a function of sampling time for ordination axis 1 (A), axis 2 (B), and axis 3 (C). Sampling time corresponds to seasons sampled (1 = summer 2002, 2 = winter 2003, 3 = spring 2003, 4 = summer 2003, 5 = winter 2004, 6 = spring 2004). Points are mean scores for all sites in a particular landuse/land cover (LULC) category (high = high forest, med = medium forest, urb = urban) for a given sampling period. Standard deviations (σ) represent the variation across time for each LULC category on each axis.

cut among our study sites (MU2, harvested within 2 y before sampling) had one of the most degraded macroinvertebrate assemblages and was an outlier in terms of biotic quality along the forest cover gradient, particularly in summer. These results underscore the differing effects of activities associated with various LULC and that observed assemblages are the result of the interplay of past and present land uses (Harding et al. 1998, Allan 2004, Maloney et al. 2008).

Which environmental variables are potential drivers of macroinvertebrate assemblages?

The assemblages with the highest biotic integrity were largely from sites with relatively low TDS and

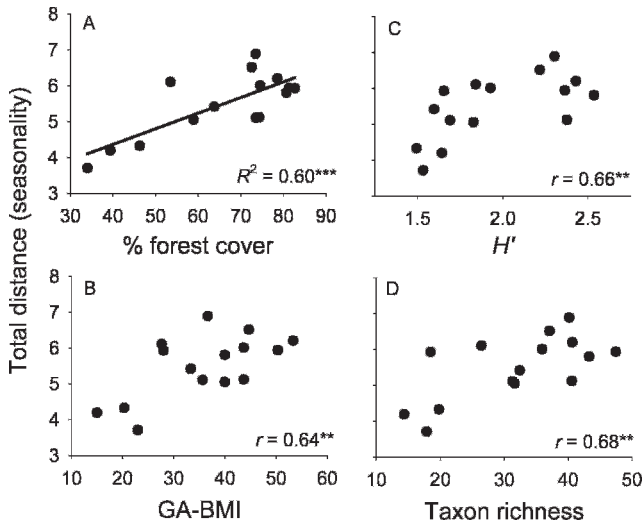


FIG. 5. Scatterplots for regression between seasonality (as total Euclidian distance in the nonmetric multidimensional scaling ordination; see *Statistical analyses* for details) and watershed % forest cover (A) and correlations between seasonality and Georgia Benthic Macroinvertebrate Index (GA-BMI) (B), Shannon diversity (H') (C), and taxon richness (D). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

high DO and proportion of detritus. Contrary to expectations, stream hydrology variables were significant predictors in only 3, and the best predictors in only 1, of the multiple regression models. This result suggests that gross hydrologic changes associated with LULC alterations, at least as we measured them, might not directly influence macroinvertebrate assemblages as strongly as changes in associated physicochemical and habitat conditions. Fine-scale reach features often are the best predictors of benthic macroinvertebrate assemblages (Richards et al. 1997, Roy et al. 2003, Strayer et al. 2003), but our results are counter to those of other studies in which altered hydrologic patterns strongly affected aquatic biota (Freeman et al. 2001, Roy et al. 2005, Helms et al. 2009). Because of their close association with the benthic habitat, small size, and short generation times, benthic macroinvertebrates might be more susceptible to indirect effects of altered hydrology (e.g., reduced water and habitat quality from increased runoff and spate frequency) than to the direct effects (e.g., displacement of individuals or eggs) often implicated in larger nektonic organisms (Freeman et al. 2001).

The specific hydrological phenomena critical to macroinvertebrate assemblage structure probably are fleeting and multifaceted. Thus, we might not have captured the most relevant hydrological variable. Furthermore, some physicochemical and habitat conditions that commonly track hydrological alter-

ation (e.g., TDS) might be less variable in the short term than hydrological variables, and might be better suited temporally to capture seasonal changes in macroinvertebrate assemblages than are fluctuating hydrological variables. More-frequent or longer-term sampling of macroinvertebrates and hydrological variables probably would clarify the precise effects of hydrologic alteration on macroinvertebrate assemblage structure.

As in many studies, we observed elevated TDS (or specific conductance) (Zampella 1994, Dow and Zampella 2000, Daley et al. 2009) and decreased biotic integrity (Walsh et al. 2001, Roy et al. 2003) with increased % urban area and % IS. Strong associations between TDS and biota, particularly in urban watersheds, suggest that TDS is a useful proxy for increased nonpoint pollution associated with efficient runoff and stream transport of conductive solids, as well as other anthropogenic disturbances. However, TDS concentrations in our study were not necessarily biologically significant because most biota can withstand TDS levels up to 1000 mg/L (Boyd 2000).

Influence of season on macroinvertebrate assemblages

Species presence/absence, richness, diversity, and tolerance of macroinvertebrate assemblages often vary seasonally (Minshall 1981, Rosillon 1985, Linke et al. 1999, Bêche et al. 2006). In our study, taxon richness, H' , biomass, and density were higher in spring than in other seasons. GA-BMI values were highest in summer, as were % shredders and % scrapers, which are 2 components of this index. However, relationships among macroinvertebrate metrics and LULC categories generally were consistent across seasons, a result suggesting that these metrics are robust enough to use for the purpose of regional comparison year-round.

In general, factors driving invertebrate seasonal variation include precipitation/discharge, insolation/temperature, and photoperiod, and each of these factors can influence disturbance regimes in streams (Resh et al. 1988, Wolda 1988, Bêche et al. 2006). In our study, seasonal differences in assemblages increased with % forest, and highly disturbed streams draining urban watersheds had the lowest degree of seasonality, probably because assemblages in urban streams were dominated by a few tolerant, but abundant, taxa (e.g., hydropsychid caddisflies) that were present year-round. In contrast, sensitive species with strong seasonal fluctuations (e.g., perlodid stoneflies) were proportionally more abundant in less-disturbed streams. These results suggest reduced community variability with increased anthropogenic disturbance

and homogenization, a pattern also noted in other studies (Brown 2003).

Conclusion and implications

Landscape effects were far-reaching, and some level of biotic impairment accompanied each of the common LULC disturbances in our study area. Loss of forest cover and intense urbanization appear to influence macroinvertebrate assemblages strongly in these watersheds. The interrelated influences of watershed disturbance are difficult to separate, but macroinvertebrates in these systems appear to respond most strongly to changes in water chemistry and benthic habitat conditions and only indirectly to hydrologic alterations.

Identification of specific environmental drivers of assemblage composition from watershed-scale LULC perturbations might help efforts to manage or restore stream communities and biotic integrity. In disturbed systems, particularly in urban/urbanizing watersheds, management and restoration efforts should be directed at both the reach and watershed scales (Rabeni and Sowa 1996, Walsh et al. 2005a). Reach-scale improvement of riparian and instream conditions by implementation of best management practices, riparian reconstruction, and habitat augmentations is essential to increasing biotic integrity in disturbed streams (Gore et al. 1998, Northington and Hershey 2006, Yates et al. 2007). However, reach-scale improvements are unlikely to have significant long-term effects, particularly in urban systems, unless stressors associated with hydrological influences of human alterations are addressed (Gore et al. 2001, Walsh et al. 2005a). For example, restoration techniques that reduce overland flow and pollutant inputs in urbanized watersheds enhance instream restoration efforts (Charbonneau and Resh 1992). Biologically relevant improvement in human-influenced systems will require a multiscale hierarchical approach to assessment and abatement of stressors associated with urbanization.

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