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ASSESSING INFLUENCES OF HYDROLOGY, PHYSICOCHEMISTRY, AND HABITAT ON STREAM FISH ASSEMBLAGES ACROSS A CHANGING LANDSCAPE[1]

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ABSTRACT: We evaluated the impact of land cover on fish assemblages by examining relationships between stream hydrology, physicochemistry, and instream habitat and their association with fish responses in streams draining 18 watersheds of the Lower Piedmont of western Georgia. Several important relationships between land use and physicochemical, hydrological, and habitat parameters were observed, particularly higher frequency of spate flows, water temperatures, and lower dissolved oxygen (DO) with percentage impervious surface (IS) cover, higher habitat quality with percentage forest cover, and elevated suspended solid concentrations with percentage pasture cover. Fish assemblages were largely explained by physicochemical and hydrological rather than habitat variables. Specifically, fish species diversity, richness, and biotic integrity were lower in streams that received high frequency of spate flows. Also, overall fish assemblage structure as determined by nonmetric multidimensional scaling was best described by total dissolved solids (TDS) and DO, with high TDS and low DO streams containing sunfish-based assemblages and low TDS and high DO streams containing minnow-based assemblages. Our results suggest that altered hydrological and physicochemical conditions, induced largely by IS, may be a strong determinant of fish assemblage structure in these lowland streams and allow for a more mechanistic understanding of how land use ultimately affects these systems.

(KEY TERMS: stream fishes; urbanization; hydrology; habitat; land cover.)

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INTRODUCTION

Biotic patterns in stream communities often are attributable to the combined influences of broad-scale environmental factors, regional species pool, watershed-specific processes, and local conditions (Frissell *et al.*, 1986; Poff, 1997; Fausch *et al.*, 2002). Human activities at the landscape level can affect these filters and thus have dramatic effects on stream community structure and function. In particular, watershed land use and land cover (LC) can alter local conditions by directly affecting water physicochemistry, hydrology, and instream habitat, which, separately or in combination, can influence biotic composition and ecological integrity (Lenat and Crawford, 1994; Clements *et al.*, 2000; Paul and Meyer, 2001; Allan, 2004; Schoonover *et al.*, 2006).

Increased levels of agriculture and urbanization in watersheds can lead to several significant effects in

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many stream features. In general, agricultural and urbanized land has been implicated in increased streamwater pollutants, decreased riparian cover, elevated water temperatures, altered hydrology, increased storm flows and sedimentation, and overall reduced habitat quantity and quality (Paul and Meyer, 2001; Allan, 2004). All of these impacts have been shown to decrease biotic integrity, such as reducing species richness, increasing physiological stress, and causing assemblage shifts (Scott *et al.*, 1986; Weaver and Garman, 1994; Schleiger, 2000; Walters *et al.*, 2003; Helms *et al.*, 2005; Roy *et al.*, 2005a).

Of the multiple direct abiotic consequences watershed land use has on receiving streams, hydrological alteration is one of the more obvious and pervasive (Booth and Jackson, 1997; Groffman *et al.*, 2003; Wang and Lyons, 2003; Walsh *et al.*, 2005). As a result of high levels of watershed imperviousness, streams draining urban and developing watersheds often display flashy hydrographs with multiple peak flows and reduced base flows (Ferguson and Suckling, 1990; Rose and Peters, 2001; Schoonover *et al.*, 2006). Storm flows often increase in magnitude and frequency in agricultural settings because of the use of drainage ditches, loss of wetlands, and soil compaction (Peterson and Kwak, 1999; Allan, 2004). Such hydrological alteration can have far-reaching effects on instream conditions. Increased peak flows can accelerate geomorphic changes in stream channels, leading to increased sedimentation, scour, and channelization, the combination of which may reduce biotic habitat quality and quantity (Wolman, 1967; Hammer, 1972; Bledsoe and Watson, 2001). In addition, stormwater runoff in urbanized watersheds often elevates concentrations of chemical pollutants, including nutrients, metals, pesticides, and pharmaceuticals (Paul and Meyer, 2001; Kolpin *et al.*, 2002; Wang and Lyons, 2003), and water temperature. Changes in temperature may cause thermal pulses and altered thermal regimes in receiving waters, which can increase mortality of sensitive species and skew assemblages towards tolerant species (Galli, 1991; Wang *et al.*, 2000; Krause *et al.*, 2004).

Conceptually, watershed LC can directly alter hydrological regimes which in turn can lead to degradations in physicochemical and geomorphic conditions. Watershed LC also can directly influence physicochemical (e.g., point-source pollution) and geomorphic conditions (e.g., livestock trampling). Altered hydrological regimes can then directly or indirectly influence biota through the alterations in physicochemical and geomorphic conditions.

Previously, we described the relationships between urbanization and fish assemblage structure in streams of western Georgia (Helms *et al.*, 2005). There we reported that declines in biotic integrity and assemblage shifts were associated with watershed LC as well as broad environmental features in high flow seasons. We suspected that differences in hydrographs across these watersheds were important in explaining fish assemblages. This study was designed to investigate the association of LC and altered hydrology on stream fish assemblages in more detail. Specifically, we examined the direct relationships among (1) watershed LC and physical instream factors (hydrology, habitat, and water physicochemistry) and (2) physical instream factors with fish assemblages. Our objective was to determine relative explanatory power of hydrology, physicochemistry, and habitat variables associated with LC change on variation in fish assemblages.

STUDY AREA

We studied stream reaches from tributaries of the middle Chattahoochee River, western Georgia, occurring in the Southern Outer Piedmont ecoregion (Griffith *et al.*, 2001). Currently, conversion of pasture and forests to urbanized areas is occurring rapidly northeast of the city of Columbus, Muscogee County. Therefore, we sampled streams draining 18 watersheds (4-25 km^2) that varied in their land use and LC from the geologic fall line in the city of Columbus to an area 80 km northeast (Muscogee, Harris, Troup, and Meriwether counties, Figure 1). Watersheds were picked based on their predominant LC in an attempt to represent the major LC disturbances in the area as well as ease of access and permission to sites. All study streams (one per watershed) were second to third order and typical of the lower Piedmont, consisting of sandy-bottom channels with run-pool morphologies (Mulholland and Lenat, 1992). LC in watersheds ranged from urban and active suburban development to pasture to heavily forested areas (Table 1). This relatively large range in landscape character allowed comparison across geomorphically similar streams that differed primarily in watershed-level LC and associated variation in streamwater physicochemical conditions.

METHODS

Land Cover Analysis

We determined watershed boundaries and size from U.S. Geological Survey 30-m resolution digital

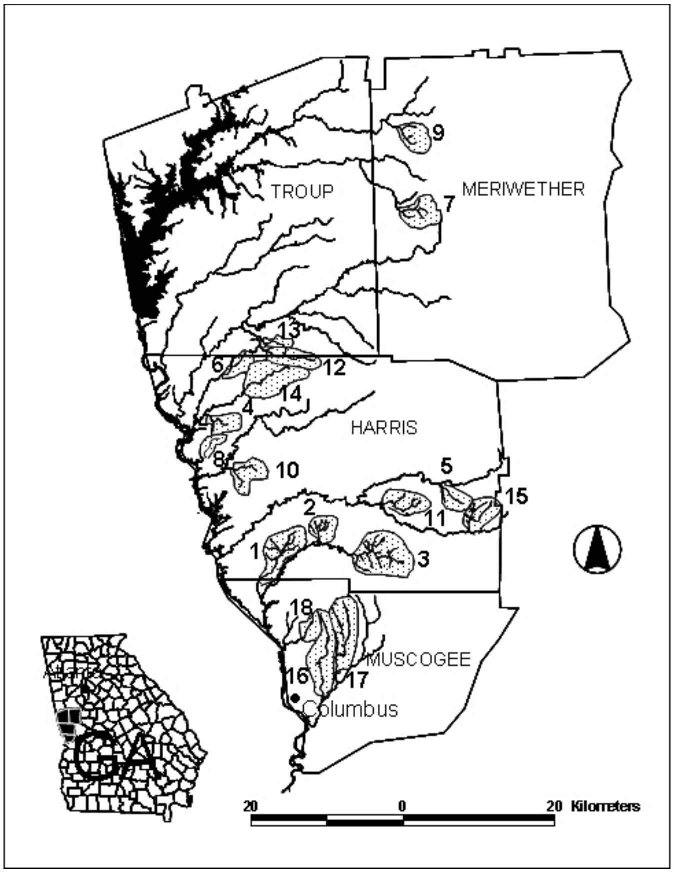

FIGURE 1. The Study Area Included 18 Small Watersheds (shaded) of the Chattahoochee River Basin in Four Counties in the Lower Southern Piedmont Ecoregion. The city of Columbus is located in western Muscogee County. County names are in capital letters. Numbers refer to watersheds and correspond to Table 1.

elevation models and ArcView 3.2a software (Environmental Research Systems Institute, Inc., Redwoods, California). True color (3 band) aerial photographs of study watersheds were taken in March 2003 during leaf-off to determine LC. Impervious surface (IS) and water bodies were manually digitized and the remaining LC was classified using a hybrid unsupervised/supervised classification scheme, a modification of the Anderson Classification Scheme (Myeong *et al.*, 2001; Lockaby *et al.*, 2005). Watersheds were ground-truthed to verify LC classes, and the overall classification accuracy (all LCs combined) was 91% (see Lockaby *et al.*, 2005 for method). We used percentage of each watershed as IS, pasture, and forest (deciduous + evergreen) for analyses. We also assigned each watershed to one of four broad LC categories to aid in describing any perceived differences among watersheds (urban, developing, pasture, and forest) (Table 1). These categories were based on the dominant LC in the watershed (percentage IS, pasture, and forest) from LC analysis except for developing watersheds, which were heavily forested but contained active residential development.

Hydrology Measures

We quantified continuous stream discharge (Q) from July 2003 to July 2004 using a Mini-Troll® pressure transducer data logger (In-Situ Inc., Ft. Collins, Colorado) housed in PVC pipe and installed near the outflow point of each watershed. We set data loggers to record a stage reading at 15-minute

TABLE 1. Land Cover and Physical Characters of Study Watersheds.

ID	Site	Stream	Watershed Size (km^2)	IS	Pasture	Forest	LC
1	SB1	Schley Creek	20.1	2	20	73	Developing
2	SB2	Standing Boy Creek Tributary	6.3	3	20	73	Developing
3	SB4	Standing Boy Creek	26.6	3	28	64	Developing
4	HC	House Creek Tributary	6.6	1	20	75	Forest
5	MU2	Mulberry Creek Tributary	6.1	1	9	82	Forest
6	SC	Sand Creek	9.0	1	21	74	Forest
7	BC	Beech Creek	6.5	2	13	81	Forest
8	BLN	Blanton Creek	3.6	1	19	76	Forest
9	MK	Flat Creek Tributary	6.6	2	20	74	Forest
10	MO	Cline's Branch	9.0	2	13	81	Forest
11	MU3	Turntime Branch	10.4	2	15	78	Forest
12	FS2	Wildcat Creek Tributary	14.5	3	36	59	Pasture
13	FS3	Wildcat Creek Tributary	3.0	3	34	62	Pasture
14	HC2	House Creek	14.1	2	44	52	Pasture
15	MU1	Ossahatchie Creek Tributary	12.0	4	37	53	Pasture
16	BU1	Lindsey Creek	25.5	40	23	34	Urban
17	BU2	Cooper Creek	24.7	25	25	46	Urban
18	RB	Roaring Branch	3.7	30	27	39	Urban

Notes: Forest, percentage managed and unmanaged forest cover; IS, percentage impervious surface cover; LC, dominant land cover in watershed; Pasture, percentage pasture cover.

intervals (0.01-m depth resolution) and then, by correlating these stage readings with discharge either directly measured or calculated at various stages (Gordon *et al.*, 2004), we developed stage-Q rating curves for each watershed to estimate continuous Q (Schoonover *et al.*, 2006). We characterized five separate elements of Q from each hydrograph (Table 2): (1) base flow, (2) predictability, (3) duration, (4) magnitude, and (5) frequency (Poff and Ward, 1989; Richter *et al.*,1996; Poff *et al.*, 1997; McMahon *et al.*, 2003).

We predicted base flow for each watershed using a 5-d smoothed minima technique (Gustard *et al.*, 1992; Schoonover *et al.*, 2006), calculated by dividing the Q data into non-overlapping 5-d blocks and determining the minimum flow in each block. The minimum value in a given block was compared with the minimum values of the previous and subsequent 5-d blocks (Gustard, 1992). If the minimum value was less than these adjacent values, it was considered an estimate of base flow for that period. Then, we used linear interpolation between each base flow estimate to predict base flow for each observed flow measure for the entire dataset. We then developed a base-flow index measure of overland flow (BI) as

$$\mathrm{BI} = \sum \text{predicted base-flow} / \sum \text{observed flow}. \quad (1)$$

Base-flow index values can range from 1, when 100% of observed Q was from base flow (low overland contribution) to 0 when 0% of observed Q was from base flow (high overland contribution, see Gustard *et al.*, 1992; Schoonover *et al.*, 2006). Ultimately, we calculated 29 hydrological variables considered

TABLE 2. List of Hydrological Variables Used in Analyses, Their Range of Values, and Significant Pearson Correlations to Predominant Land Cover Classes in the 18 Watersheds.

Variable ID	Description	Range	IS	Forest	Pasture
Magnitude					
MedQ	Median discharge (l/s)	0.01-0.90			0.49*
MaxQ	Maximum discharge (l/s)	0.54-21.98			
MinQ	Minimum discharge (l/s)	0-0.38			
	Frequency (number of times exceeded threshold)				
3× Med	Number of times discharge exceeded 3× median flow	5-116			
5× Med	Number of times discharge exceeded 5× median flow	1-70	0.50*		
7× Med	Number of times discharge exceeded 7× median flow	1-64	0.56*		
9× Med	Number of times discharge exceeded 9× median flow	0-58	0.58*		
>75th	Number of times discharge exceeded 75th percentile	25-115			
>95th	Number of times discharge exceeded 95th percentile	12-66			
>99th	Number of times discharge exceeded 99th percentile	2-35	0.62**		
	Duration (number of hours spent above threshold)				
>3× Med_d	Hours discharge was >3× median flow	36.5-3,026			
>5× Med_d	Hours discharge was >5× median flow	6-2,518			
>7× Med_d	Hours discharge was >7× median flow	1.5-2,412			
>9× Med_d	Hours discharge was >9× median flow	0-17			
Predictability and Flashiness					
C.V.	% Coefficient of Variation	42-402			
Inc1h100	Number of events discharge increases by 100% within 1 hour	7-109	0.55*		
Inc1h1000	Number of events discharge increases by 1,000% within 1 hour	0-31			
Inc1h5000	Number of events discharge increases by 5,000% within 1 hour	0-17			−0.47*
Inc3h100	Number of events discharge increases by 100% within 3 hours	11-122	0.53*		
Inc3h1000	Number of events discharge increases by 1,000% within 3 hours	0-44			
Inc3h5000	Number of events discharge increases by 5,000% within 3 hours	0-19			
Dec1h100	Number of events discharge decreases by 100% within 1 hour	0-67			
Dec1h1000	Number of events discharge decreases by 1,000% within 1 hour	0-28			
Dec1h5000	Number of events discharge decreases by 5,000% within 1 hour	0-12			
Dec3h100	Number of events discharge decreases by 100% within 3 hours	1-92			
Dec3h1000	Number of events discharge decreases by 1,000% within 3 hours	0-36			
Dec3h5000	Number of events discharge decreases by 5,000% within 3 hours	0-18			
Base flow (l/s)					
Med_bf	Median base flow (l/s)	0.04-730			
BI	Base-flow index ($\sum$ predicted base flow/$\sum$ observed flow)	0.03-0.82			

Notes: Forest, proportion of forest (managed + unmanaged) cover; IS, proportion of impervious surface cover; Pasture, proportion of pasture cover; PCA1 and PCA2, Principal Components Analysis axes 1 and 2, respectively.
*p < 0.05 and **p < 0.01.

important in describing stream biotic parameters (Richter *et al.*, 1996; Poff *et al.*, 1997; Roy *et al.*, 2005a) for each watershed (Table 2). Historical hydrographs were unavailable for these watersheds thus temporal changes with LC change were not assessed.

Physicochemistry Measures

We measured several physicochemical variables over the hydrological period of record (Table 3). Stream temperature was measured continuously with HOBO® temperature data loggers (ONSET Computer Corporation, Pocasset, Massachusetts) placed near the pressure transducers. Dissolved oxygen (DO) was measured seasonally (four times over period of record) in all habitats where fish were sampled with a YSI 55 handheld meter (YSI Incorporated, Yellow Springs, Ohio). Total suspended solid concentrations (TSS) were determined monthly from grab samples using gravimetric filtration methods (USEPA, 1999). Total dissolved solid concentrations (TDS) and pH were also determined monthly from grab samples using a Fisher Accumet AR20 pH/conductivity meter (Fisher Scientific, Pittsburg, Pennsylvania).

Fish and Habitat Sampling

We sampled stream fish assemblages in June 2004 from three run and three pool habitat units per stream (habitat units spanned the width of the stream) along a representative 100-m reach. Reaches were selected based on maximizing the subjective quality of common habitats in the stream and were located at least 100 m above or below any bridge crossing. Stratifying fish sampling in quality run and pool habitats of the reach maximized field crew efforts and resulted in, on average, 50% of the linear distance of the reach being sampled. Previous collections in this area have revealed increased abundances in summer months but no seasonal difference in species richness, justifying June sampling (Helms, 2008). We sampled fish in each habitat to depletion with block nets and a Smith-Root LR-24 backpack electroshocker (Smith-Root, Inc, Vancouver, Washington) and supplemented larger habitats with seining. We identified and measured total length of all fish captured and returned them near the point of collection, except for voucher specimens of each species, which were deposited in the Auburn University Museum Fish Collection.

We assigned species to feeding and reproductive guilds (Muncy *et al.*, 1979; Berkman and Rabeni, 1987), as they have been shown by others to be reliable indicators of biotic integrity in Georgia piedmont streams (Schleiger, 2000; Helms *et al.*, 2005). For feeding guilds, fish were classified as piscivores, insectivores, herbivores, omnivores, or filter feeders. For reproductive guilds, we initially classified fish as complex or simple breeders, based on the degree to which species prepare spawning sites, defend nests, and show prespawning social behavior (Pflieger, 1975; Trautman, 1981). Complex breeders were then further classified into those species that show parental care (P/C) and those that do not (No P/C). Simple breeders were divided into spawners requiring clean, gravel substrate (lithophilic spawners, =Lithophils) and those capable of spawning on sand, silt, or vegetation (generalist spawners, =Simple Spawners). We used these classifications to assess whether there were functional changes in assemblages associated with different stream conditions.

TABLE 3. Physicochemical and Habitat Variables Used in Analyses, Their Range of Values, and Significant Pearson Correlations to Predominant Land Cover Classes in the 18 Watersheds.

Variable ID	Description	Range	IS	Forest	Pasture
Temp	Median water temperature (°C)	13.3-15.6	0.67**	−0.54*	
DO	Mean dissolved O_2 (mg/l)	8.6-14.5	−0.50*		
minDO	Minimum dissolved O_2 (mg/l)	0.2-8.3			
pH	Mean pH	5.7-6.9			
TDS	Mean total dissolved solids concentration (mg/l)	19.9-58.6	0.58*		
TSS	Mean total suspended solids concentration (mg/l)	2.1-8.1			0.54*
Volume	Mean depth × width × length of habitat sampled (m^3)	0.6-6.9	0.76***	−0.65**	
OM	Benthic organic matter (g)	0.3-1.2		0.47*	
Substrate	Median substrate size (cm)	0.5-1.8	0.52*		
T_G	Tractive force	2.7-73.9			
Habitat Index	Habitat assessment index score	54.2-125.5		0.48*	

Notes: Forest, proportion of forest cover (managed + unmanaged); IS, proportion of impervious surface cover; Pasture, proportion of pasture cover.
*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

We calculated species richness and species diversity (Shannon's H') for each stream. Richness and H' are commonly used metrics for comparing fish assemblages; however, human disturbance may cause only nominal changes in H' or species richness but major changes in species composition (Scott and Helfman, 2001; Walters *et al.*, 2005). Therefore, we also calculated a stream-specific index of biotic integrity (IBI) modified for Georgia piedmont streams (Schleiger, 2000) and relative abundance for use in a nonmetric multidimensional scaling (NMDS) ordination to describe overall variation in fish assemblages among watersheds.

To assess available habitat quality and quantity, we used a comprehensive multimetric habitat assessment from the Georgia Department of Natural Resources, Environmental Protection Division (GA DNR) designed for use in fish biomonitoring (GA DNR, 2005). This Habitat Index included visual estimates of available cover (number and frequency of habitat types), substrate characterization (type and condition), pool morphology (shape and frequency), channel alteration (frequency of riprap, dredging, etc.), channel sinuosity (run-to-bend ratio), sediment deposition (particle, point bar, and island size), flow status (degree to which channel is filled with water), bank condition (erosion potential and vegetation cover), and riparian condition (vegetation cover and quality) (GA DNR, 2005). This assessment involves taking the average of three individuals' summed scores (1-10 or 1-20, depending upon parameter) of the different habitat parameters to obtain an overall habitat quality value for the representative reach, with high average score indicating high habitat quality. We used the same three observers at all sites.

In addition to the GA DNR habitat assessment, we assessed stream habitat by quantifying habitat volume (mean depth $\times$ width $\times$ length), benthic organic matter abundance (BOM), substrate particle sizes, and benthic shear stress (T_G) in each habitat unit at the time of fish sampling. Habitat volume was measured in every habitat fish sampled along the reach and averaged for the stream as an assessment of the size of the habitats being used. We estimated BOM and substrate size by sampling transitional areas between the runs and pools where fish were sampled to standardize our efforts and avoid error associated with scour in the runs and deposition in the pools. We sampled BOM by determining the ash-free dry mass of nine replicate 2.5×10 cm benthic cores. For substrate particle size, we collected three benthic samples per stream (near where BOM was sampled) using a 76.2-mm diameter PVC substrate core to a depth of 10 cm. We dried samples and separated particles into five 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 (0.05-0.1 mm), and silt/clay (<0.05 mm) to determine median substrate size by weight (USDA, 1951). We estimated T_G close to where pressure transducers were located using

$$T_G = pgRS, \tag{2}$$

where p is the density of water, g is gravitational acceleration, R is hydraulic radius, and S is energy slope (Gore, 1996).

DATA ANALYSES

First, we used simple Pearson correlations to examine relationships between environmental variables (hydrology, habitat, and physicochemical) and LC. All continuous variables were log-transformed and percent variables were arcsine-square root transformed as needed to meet assumptions of normality (Zar, 1999).

Second, we used NMDS to describe overall variation in fish assemblages among sites. NMDS is an ordination technique that handles data with many zeroes and nonnormal data better than other ordination techniques such as Principal Components Analysis (PCA, McCune and Grace, 2002). Unlike PCA, the order of the axes in the resultant ordination does not necessarily imply the order of greatest variation explained. We transformed proportional relative abundance data using arcsin-square root and excluded rare species (those in <10% of sites) to reduce the influence of rare taxa on ordinations. This step resulted in an 18×23 site species matrix on which we based ordinations using a Sorenson distance measure (McCune and Grace, 2002). We correlated all environmental variables and fish assemblage variables to the resulting NMDS ordination to assess spatial differences among watersheds.

Last, we used stepwise multiple regression analyses ($p = 0.05$ to enter and leave the model) to determine which environmental variables, directly or indirectly related to LC, had the most explanatory power in regards to fish assemblages. To ensure that observed trends were a result of landscape disturbance, any hydrologic variable not related to some aspect of LC was dropped from multiple regression as were any physicochemical or habitat variable not related to either LC or the selected hydrologic variables. In order to avoid multicollinearity among predictors, all parameters in the final models had a variance inflation factor <10 (Myers, 1990).

RESULTS

Stream Hydrology

In general, the hydrographs of the urban and developing watersheds were flashier and less stable than hydrographs in other watersheds (Table 2). There was a strong relationship between urbanization and the frequency and predictability of hydrological events as evidenced by several parameters being positively correlated with IS, notably the measures 5× Med, 7× Med, 9× Med, and N > 99th and the variables Inc1h100 and Inc3h100 (Table 2). Median Q also was positively correlated and Inc1h5000 was negatively correlated with proportion of watershed as pasture. There was no significant relationship between any hydrological parameter and proportion of watershed as forest (Table 2). We therefore used these eight hydrologic variables (5× Med, 7× Med, 9× Med, N > 99th, Inc1h100, Inc3h100, Inc1h5000, and Median Q) in subsequent multiple regressions since they showed significant relationships with some aspect of watershed LC.

Physicochemistry and Habitat

Physicochemical and habitat parameters were variable across the watersheds with all parameters associated with either watershed LC and/or hydrology (Tables 3 and 4). In general, higher stream temperatures and lower DO levels were associated with increased watershed IS and spate flows (5× Med, 7× Med, and 9× Med, Tables 3 and 4). Mean and minimum DO levels were highly correlated with each other (r = 0.884, p < 0.001), and since mean DO was a continuous measure and minimum DO was a single measurement, we used mean DO for statistical analyses. Further, TDS was positively associated with IS cover and spate frequency measures, TSS was positively correlated with percentage pasture and the flashiness variable Inc1h5000, and pH was positively correlated with Inc1h100 and Inc3h100 (Tables 3 and 4). Of the habitat variables considered, habitat volume and median substrate size were positively correlated with IS while organic matter and the Habitat Index were positively correlated with forest cover (Table 3). Substrate size was also positively correlated with spate frequency variables, tractive force increased with median discharge, and the Habitat Index increased with Inc1h5000. As all physicochemical variables were correlated with either a hydrologic or LC variable, they were all included in multiple regressions analysis.

Fish Assemblage Structure

We collected 27 fish species (1,152 individuals) in seven families during the study, with Cyprinidae (minnows) and Centrarchidae (sunfishes) being the most common and abundant families (Table 5). Of the breeding and feeding guilds, proportion of lithophilic spawners declined with increasing IS (r = −0.66, p < 0.01) and increased with total forest cover (r = 0.51, p < 0.05) while proportion of insectivores increased with IS (r = 0.57, p < 0.05) and decreased with forest cover (r = −0.51, p < 0.05). Species richness ranged from 2 to 13 species, with highest measures in pasture and forested watersheds, and was negatively correlated with IS (r = −0.66, p < 0.01) (Table 6). H' ranged from 1.07 to 2.95, with the highest values in forested and pasture dominated watersheds, and was negatively correlated with IS (r = −0.85, p < 0.01) and positively correlated with forest cover (r = 0.52, p = 0.03), while proportion of sunfish increased with urban cover (Table 5). IBI values ranged from 22 to 42,

TABLE 4. Associations Between Select Hydrologic Variables and Environmental Variables.

	Hydrologic						
Environmental	**MedQ**	**5× Med**	**7× Med**	**9× Med**	**Inc1h100**	**Inc1h5000**	**Inc3h100**
Temp		0.55*	0.66**	0.69**	0.48*		
DO		−0.59*	−0.69**	−0.72**			
pH					0.76***		0.73**
TDS		0.78***	0.84***	0.85***			
TSS						−0.69**	
Substrate		0.72**	0.74***	0.73**	0.53*		0.48*
T_G	0.52*						
Habitat Index						0.55*	

Notes: DO, dissolved oxygen; TDS, total dissolved solid; TSS, total suspended solid.
Values are Pearson correlation coefficients, and only those with a significant correlation are shown.
*p < 0.05, **p < 0.01, and ***p < 0.001.

TABLE 5. Fish Families and Species Collected From 18 Study Watersheds, Common Name, Breeding and Feeding Guilds, and Pearson Correlation Coefficients to NMDS Axes 1 and 3.

Family	Species	Common Name	Breeding	Feeding	$NMDS_1$	$NMDS_3$
Catastomidae	*Erimyzon oblongus*	Creek chubsucker	S	I	0.38	0.18
	Hypentelium etowanum	Alabama hog sucker	L	I	0.12	0.22
	Minytrema melanops	Spotted sucker	L	I	–	–
Centrarchidae	*Lepomis auritus*	Redbreast sunfish	Cpc	I	−0.37	0.72
	L. cyanellus	Green sunfish	Cpc	I	−0.39	0.19
	L. gulosus	Warmouth	Cpc	P	−0.29	−0.34
	L. macrochirus	Bluegill	Cpc	I	−0.52	−0.55
	L. megalotis	Longear sunfish	Cpc	I	−0.39	−0.43
	L. miniatus	Redspotted sunfish	Cpc	I	0.06	0.22
	Micropterus salmoides	Largemouth bass	Cpc	P	−0.29	0.13
Cyprinidae	*Campostoma pauciradii*	Bluefin stoneroller	Cnc	H	0.04	0.06
	Luxilus zonistius	Bandfin shiner	L	I	0.81	0.24
	Nocomis leptocephalus	Bluehead chub	Cnc	O	0.82	0.17
	Notemigonus crysoleucas	Golden shiner	S	I	−0.35	−0.30
	Notropis baileyi	Rough shiner	L	I	0.65	−0.19
	N. buccatus	Silverjaw minnow	S	I	0.19	−0.37
	N. longirostris	Longnose shiner	L	L	0.48	−0.11
	N. texanus	Weed shiner	S	I	−0.43	−0.12
	Semotilus atromaculatus	Creek chub	Cnc	O	0.61	0.07
Ictaluridae	*Ameirus natalis*	Yellow bullhead	Cpc	O	−0.40	0.16
	A. nebulosus	Brown bullhead	Cpc	O	0.07	0.37
	Ictalurus punctatus	Channel catfish	Cpc	O	–	–
	Noturus leptocanthus	Speckled madtom	Cpc	I	–	–
Percidae	*Percina nigrofasciata*	Blackbanded darter	L	I	−0.17	−0.29
Petromyzontidae	*Ichthyomyzon gagei*	Brook lamprey	Cnc	F	0.38	0.37
Poeciliidae	*Gambusia affinis*	Western mosquitofish	Cnc	I	−0.43	0.14

Notes: NMDS, nonmetric multidimensional scaling.
Rare species excluded from NMDS analyses are denoted by dashes.
Breeding guild abbreviations: Cnc, complex with no parental care; Cpc, complex with parental care; L, simple lithophil; S, simple miscellaneous.
Feeding guild abbreviations: F, filterer; H, herbivore; I, insectivore; O, omnivore; P, predator.

with highest values in pasture and forested watersheds; however, the IBI was not significantly correlated with any LC parameter.

Nonmetric multidimensional scaling axes 1 and 3 ($NMDS_1$ and $NMDS_3$) were the two axes describing the most variation in fish assemblages among streams (48.7% and 22.8%, respectively; stress = 13.8, instability = 0.00001, iterations = 91; Figure 2). Streams in Urban and Developing watersheds generally grouped to the left of the ordination whereas streams from Forest and Pasture watersheds grouped mostly to the right (Figure 2). Number of fish collected, H', proportion of lithophils, and IBI all were positively correlated with $NMDS_1$ while the proportion of sunfish, insectivores, and fish showing no parental care, were all negatively correlated with $NMDS_1$ (Figure 2). The proportion of the assemblage showing parental care was significantly correlated with $NMDS_3$ (Table 6). There were several environmental parameters associated with these shifts in fish assemblage structure across the landscape, including stream DO levels, water temperature, TDS, substrate size, frequency of spate flows, and habitat volume (Figure 2).

Relative Influence of Environmental Variables on Fish Assemblages

Multiple regression analyses revealed that hydrologic and physicochemical variables were good predictors of fish assemblages (Table 7). Models describing richness, diversity, and the IBI all contained measures of spate frequency (5× Med, 7× Med, and N > 99). Streamwater temperature was the best predictor of number of fish collected while temperature and 5× Med best described taxa richness (Table 7). TDS was also prominent in models as a strong predictor of diversity and percentage sunfish (Table 7). No habitat variables were included as parameters in any best models.

DISCUSSION

Environmental controls of stream fish assemblages are varied, often interactive, and frequently associated with landscape disturbance (Roth *et al.*, 1996;

TABLE 6. Fish Metrics and Their Correlations
Watershed LC and Best NMDS Axes.

Metric	IS	Forest	Pasture	$NMDS_1$	$NMDS_3$
Breeding					
Parent Care					0.78***
No Parent Care				−0.61**	
Simple					
Lithophilic	−0.66**	0.51*		0.87***	
Feeding					
Piscivore					
Insectivore	0.57*	−0.51*		−0.57*	
Herbivore					
Omnivore				0.61**	
Filterer				0.50*	
Assemblage					
Number				0.50*	
Richness	−0.66**			0.46*	
Diversity	−0.85***	0.52*		0.55*	
Percentage Sunfish	0.58*			−0.75***	
IBI				0.48*	

Notes: Forest, proportion of forest cover; IBI, index of biotic integrity; IS, proportion of impervious surface cover; LC, land cover; NMDS, nonmetric multidimensional scaling; $NMDS_1$ and $NMDS_3$ are NMDS axes 1 and 3, respectively; Pasture, proportion of pasture cover.
Only significant correlations are shown.
Fish metrics are as described in text.
$^{*}p < 0.05$ and $^{**}p < 0.01$.

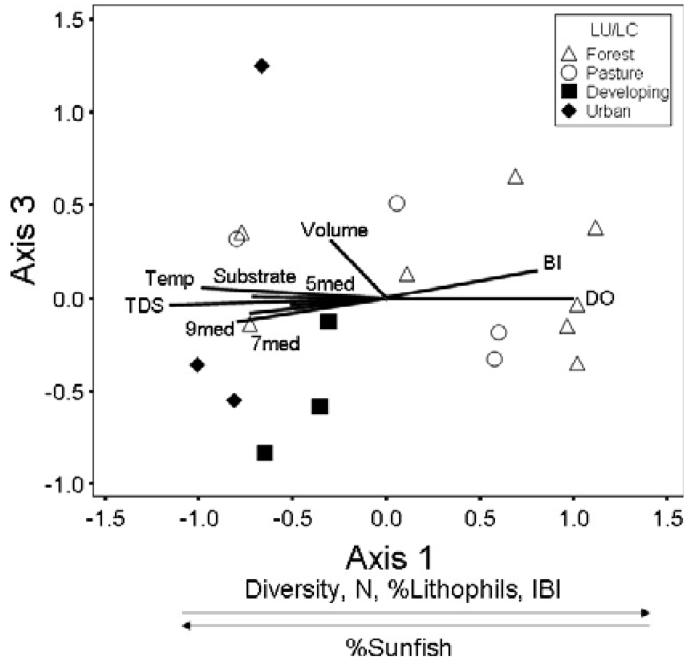

FIGURE 2. Nonmetric Multidimensional Scaling Ordination of Sites in Ordination Space. Axes are scaled proportionate to the longest axis (percentage of max). Symbols are the 18 study sites coded by land use classifications as described in text with vectors that show relative direction and strength of correlated environmental variables. Arrows on x and y axes show direction of correlated fish assemblage values. Axes 1 and 3 explained 57.1 and 25.3% of the total variation, respectively. For vector labels, DO, dissolved oxygen; BI, base-flow index; Volume, habitat volume; 5med, number of hydrological events greater than 5× median flow; 7med, number of hydrological events greater than 7× median flow; 9med, number of hydrological events greater than 9× median flow; Substrate, median substrate size; Temp, median stream temperature; and TDS, total dissolved solids.

Matthews, 1998; Lammert and Allan, 1999). Our results provide additional empirical evidence that the indirect effects of land use on the integrity of fish assemblages can occur through the alteration of instream environmental conditions, particularly alterations in hydrological and physicochemical conditions.

Influence of Hydrology on Fish Assemblages

Streamflow is often considered the master variable limiting aquatic biota by its effects on instream physicochemistry, geomorphology, and habitat diversity (Poff and Allan, 1995; Poff *et al.*, 1997). In the study streams, hydrology appeared to have a strong effect on differences in fish assemblages among watersheds. Richness, H', and IBI all were lower in streams experiencing numerous high-magnitude flows, whereas more taxonomically rich and diverse assemblages were associated with streams experiencing fewer high-magnitude flows. Fish patterns were also strongly associated with the number of events that exceeded five, seven, and nine times median flow, moderate events that, on average, were all less than 33% of bankfull Q in these watersheds. Small, frequent spates have been suggested to be more important than infrequent larger events in causing ecological impacts (Walsh *et al.*, 2005). Moreover, BI was a strong correlate of NMDS axis 1, suggesting that increases in overland flow events and associated

TABLE 7. Best Multiple Regression Models for Fish Assemblage Variables With Standardized Regression Coefficients and R^2_{adj}.

Metric	Predictors	Standardized Estimate	R^2_{adj}
N	Temp	−0.58	0.29**
Richness	5× Med	−0.68	0.43**
	Temp	−0.40	
Diversity	TDS	−0.54	0.54***
	N > 99	−0.40	
Percentage Sunfish	TDS	0.73	0.48**
	MedQ	0.43	
IBI	7× Med	−0.52	0.22*

Notes: IBI, index of biotic integrity; TDS, total dissolved solid.
Fish metric definitions are as in text.
Predictor definitions are as in Tables 2 and 3.
$^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$.

spate frequency, and not necessarily alterations in the duration, predictability, or magnitude of flows, are strong hydrological drivers of fish assemblages in these watersheds. These findings support other studies on fish reporting increased proportions of habitat generalist species with increasing frequency of hydrological disturbance, and taken together, underscore the far-reaching effects of hydrology on stream ecological integrity (Resh *et al.*, 1988; Poff *et al.*, 1997; Freeman *et al.*, 2001; Roy *et al.*, 2005a). If true for other piedmont watersheds, then such frequency-based hydrological variables should be taken into consideration by resource managers to identify flow-related impacts to fish in developed and developing watersheds.

As shown by others, fish assemblages overall show lower diversity and integrity in developing and highly urbanized watersheds compared with less-developed watersheds (Koel and Peterka, 2003; Walters *et al.*, 2003; Helms *et al.*, 2005; Roy *et al.*, 2005a). However, it should be noted that, since urbanization patterns are often spatially clumped (Brown *et al.*, 2005), similarities in fish assemblages could be attributable to factors not considered here (e.g., species ranges, biogeography, etc.). For instance, in our study weed shiners (*Notropis texanus*), generally considered a coastal plain species, were rarely found outside of the urban and developing watersheds, a pattern likely resulting from these watersheds being at the periphery of this species' range (Boschung and Mayden, 2004). Yet these watersheds, which are biogeographically similar in terms of fish assemblages, were well within the geographic range of all other fish species detected (Swift *et al.*, 1986; Boschung and Mayden, 2004).

As determined from the NMDS ordination, the observed spatial pattern of fish appeared to correspond to the combined changes in stream hydrological and physicochemical conditions associated with increasing IS and connectedness in the urban and developing watersheds. Interestingly, BI was not significantly correlated to any LC variable, likely offset by the relatively high percentage forest in the developing streams, demonstrating the pervasive impact of urbanization. In a related study of these same sites (Schoonover *et al.*, 2006), measures of BI suggest that overland flow (*vs*. base-flow inputs) contributed up to 90% of Q reaching Urban streams and 65 to 90% of Q reaching Developing streams. High overland flow and associated spates are not only likely to contribute significant physical impacts on fishes (i.e., through downstream displacement of individuals, habitat alterations, etc.), but can also act to transport pollutants; elevate water temperatures, bacteria, and nutrient concentrations from terrestrial sources; and also resuspend materials in the stream bed (Casey and Farr, 1982; Paul and Meyer, 2001).

In the study streams, TDS and temperature was generally elevated and DO decreased in urbanized systems and associated with decreased fish diversity. Many other studies have also observed elevated TDS (or specific conductivity) with increased urban area or IS (Dow and Zampella 2004) as well as with decreased biotic integrity (Walsh *et al.*, 2001; Roy *et al.* 2003). However, TDS concentrations were not necessarily at biologically significant levels, as most aquatic systems with biota can withstand TDS levels up to 1,000 mg/l (Boyd, 2000). Therefore, the strong association of TDS with developing and urbanized watersheds suggests that it is a likely indicator of increased nonpoint pollution associated with efficient runoff, thus an "anthropogenic marker" in these streams.

Water temperature and DO are major regulators of fish distribution, growth, migration, and survival (Fry, 1947; Regier *et al.*, 1990; Smale and Rabeni, 1995; Krause *et al.*, 2004), and levels of each of these parameters are important predictors of fish assemblages in streams of western Georgia. Warm water sunfish species were present in all of our study streams, but they were far more abundant in streams with higher water temperatures and lower DO than in streams without these stressors. This pattern suggests that elevated stream temperature and low DO, particularly in urban and developing streams with reduced riparian cover and receiving thermally enhanced overland flow (Van Buren *et al.*, 2000; Roy *et al.*, 2005b), may negatively affect presence or abundance of fishes in general. It seems unlikely that elevated temperature directly affected fishes as the maximum water temperature we observed (25.6°C) was well below most physiological thresholds and habitat requirements for most native fish of this region (Brown, 1974; Aho *et al.*, 1986; Krause *et al.*, 2004). However, besides causing mass fish kills (Gafney *et al.*, 2000), low DO may produce important sublethal effects, leading to habitat and behavioral shifts in populations and, ultimately, altered local assemblage structure (Kramer, 1987; Matthews, 1987, 1998). Specifically, critical DO levels for similar fish assemblages in warm water streams range from 0.49 to 1.49 mg/l and strong effects of hypoxia on fish habitat use and species composition have been implicated when water DO minima fall below 4 to 5 mg/l (Smale and Rabeni, 1995). DO levels in our streams occasionally reached these lethal levels and frequently reached those reported levels that could influence species distribution over the period of record.

Altered land use can induce physical changes in stream channels, influencing the dynamics and spatial arrangement of channel features and instream habitat (Allan, 2004). Our analyses indicated that some instream fish habitat conditions were related to watershed LC. However, habitat variables in general were weak predictors of fish assemblage structure. There was a relationship between assemblage structure and substrate size as evidenced by NMDS axis 1, with more tolerant assemblages being associated with streams with large substrate size. This habitat feature is likely the result of bed coarsening and flushing, and is common in urban and other hydrologically altered watersheds (Finkenbine *et al.*, 2000; Walsh *et al.*, 2005). However, considering the size range (0.5-1.8 cm), and that lithophilic spawners were negatively associated with substrate size, substrate composition was unlikely to be an important driver of assemblages in these streams. Taken together, our results suggest that hydrological regimes may influence instream habitat conditions in these watersheds, but local habitat *per se* is not a strong driver of the observed differences in fish assemblages (*cf*. Poff *et al.*, 1997; Sutherland *et al.*, 2002). It should be noted, however, that the weak link between fish assemblages and habitat variables, compared with hydrological and physicochemical measures, may reflect a disparity of (1) scale between our measures of habitat (100-m study reaches) and potential longitudinal movement of fish (>100 m); (2) sampling, given that we measured hydrology and physicochemistry multiple times (and, for some measures, continuously) over the study, and habitat variables were measured just once; and (3) the biotic composition of fishes in general in lower Piedmont watersheds of the Chattahoochee drainage, which have a natural predominance of widespread species (Hilliard, 1984; Swift *et al.*, 1986).

CONCLUSIONS

Our results suggest that LC induced changes in hydrology and streamwater physicochemistry, particularly in developing and urbanized watersheds, influence stream fish assemblages more so than alterations in physical habitat; however, there is undoubtedly high complexity in the functional interrelationships of environmental variables in these streams. Physicochemical conditions are closely linked to hydrology and land use, and teasing the relative importance of each often can be logistically difficult. The use of multivariate analyses effectively allowed us to identify important correlates of fish assemblage structure that, as a result of the nature of the suburban landscape, were not strongly associated with measured LC values (e.g., BI). However, many physicochemical conditions are correlated, so it may only be necessary to identify a single physicochemical or hydrological group of variables (e.g., spate frequency and temperature/DO) for certain management or restoration goals. Further, in these lower Piedmont systems with a history of land use degradation, an assemblage-based response (such as the NMDS ordination) may be better suited to evaluating the impacts of human induced change than traditional metrics (e.g., H') because of the high abundance of widely distributed species and relatively few endemics, often hindering useful comparisons to degraded systems.

Human population expansion and the inevitable landscape alteration caused by such growth have produced dramatic impacts on stream ecosystems. By attempting to identify the specific hydrological and physicochemical driver(s) of biotic composition resulting from these perturbations, we can better address management and restoration needs designed to protect or minimize changes in stream biotic integrity.

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