J. N. Am. Benthol. Soc., 2006, 25(2):356–369
© 2006 by The North American Benthological Society

Physical and biological responses of streams to suburbanization of historically agricultural watersheds

Chris L. Burcher[1] AND E. F. Benfield[2]

Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0406 USA

Abstract. We investigated whether suburbanization influenced the physical and biological characteristics of ten 3rd-or 4th-order streams that drain historically agricultural watersheds in the southern Appalachians near Asheville, North Carolina. Five watersheds had areas of recent suburban development proximal to stream sites, and 5 watersheds were not currently undergoing suburban development. We estimated 5 hydrological, 10 geomorphological, 6 erosional, and 3 depositional (i.e., substrate) variables, and 13 fish and 8 macroinvertebrate metrics in the study sites. We used Student's *t*-tests and multivariate analysis of variance to compare the 45 variables between sites in agricultural and suburban watersheds. We used Detrended Correspondence Analysis (DCA) to detect subtle differences in taxonomic composition and abundance among watersheds. Stormflow total suspended solids were significantly lower and substrate inorganic matter content was significantly higher in streams influenced by suburban development. Fish taxa richness and the density of nonguarding fishes were significantly higher in sites in suburban watersheds than in sites in agricultural watersheds. No other fish or macroinvertebrate metric differed with respect to watershed land use, but ordination of sites by fish and macroinvertebrate species abundance suggested that biotic assemblages at sites in suburban watersheds were distinct from those at sites in agricultural watersheds. Therefore, some taxa may have been influenced by suburban development. Our results suggest that watershed hydrology, sediment delivery, and sediment composition might be important factors influencing biota in streams draining agricultural vs suburban watersheds. Biological assemblages in streams differed structurally with respect to watershed land use, but streams did not appear to be otherwise influenced by suburban development. We conclude that suburbanization near historically agricultural southern Appalachian streams induces subtle changes to inorganic sediment dynamics, substrate composition, and fish and macroinvertebrate assemblage structure.

Key words: streams, suburbanization, agriculture, macroinvertebrates, fish, Appalachia, land use, total suspended solids, landscape.

Anthropogenic disturbance of the landscape influences physical, chemical, and biological elements of stream ecosystems. Agricultural and urban activities include nutrient enrichment, tilling, animal grazing, chemical contamination, and building of human infrastructure, and the influences of these activities have been studied intensively for the last 30 y (Heimlich and Anderson 2001, Paul and Meyer 2001). This research has identified how hydrological (e.g., Poff and Allan 1995, Jones et al. 2000), geomorphological (e.g., Rhoads and Cahill 1999, Stanley et al. 2002), sediment (Trimble 1997), and biological (e.g., Harding et al. 1998, Wang et al. 2001, Sutherland et al. 2002) elements of streams respond to anthropogenic disturbance.

[1] E-mail addresses: cburcher@vt.edu
[2] benfield@vt.edu

Agriculture (Harding et al. 1998, Cuffney et al. 2000) and urban development (Wear et al. 1998, Paul and Meyer 2001) alter stream hydrology and geomorphology (Heimlich and Anderson 2001), enhance erosion caused by removal of rooted riparian vegetation (Neller 1988, Trimble 1997), reduce taxonomic diversity, and impair biological structure and function. In urban systems, impervious surface cover (ISC) exacerbates overland flow hydrology, so that overland flow often dominates stream hydrographs (Jennings and Jarnagin 2002, Roy et al. 2005). In agricultural systems, erosional dynamics alter the concentration of instream suspended sediments, especially during storms, and removal of watershed vegetation alters hydrologic activity, often resulting in higher maximum flows and more dynamic sediment movement than before the

TABLE 1. Names, site codes, and watershed characteristics of the 10 study streams. Land-cover data are from USGS (2002). "Other" land-cover category includes open water, wetland vegetation, and barren areas. Sub = suburban sites, Ag = historically agricultural sites not undergoing current suburbanization.

Stream	Site code	Watershed area (ha)	Stream length (km)	Land cover (%)			
				Forest	Agriculture	Urban	Other
Avery Creek	Sub1	1744	12	75	21	1	2
Brush Creek	Sub2	987	8	74	22	1	2
Hooper's Creek	Sub3	3552	28	75	22	1	2
Merril's Cove Creek	Sub4	1349	9	78	16	5	2
Robinson Creek	Sub5	1445	8	56	18	24	2
East Fork Bull Creek	Ag1	2050	15	80	19	0	1
Gabriel's Creek	Ag2	1601	14	57	36	4	3
Middle Fork Creek	Ag3	3049	23	20	75	0	4
Paint Creek	Ag4	1286	16	77	22	0	1
West Fork Bull Creek	Ag5	2015	15	76	22	0	2
Mean (±1 SE) Sub		1815 (509)	13 (4)	72 (0)	20 (1)	7 (1)	2 (0)
Mean (±1 SE) Ag		1703 (327)	14 (2)	62 (12)	35 (12)	1 (1)	2 (1)

disturbance (Bhaduri et al. 2000, Swank et al. 2001, Roy et al. 2005).

Urban sprawl is encroaching on rural areas at a global scale and is transforming agricultural landscapes to suburban systems (Meyer and Turner 1992, Hunter 2000, Ramankutty et al. 2002). The United Nations predicts that 85 to 90% of projected world population growth between 2000 and 2030 will occur as urban sprawl (United Nations 1999). We call this process of suburban encroachment on rural landscapes in North America *suburbanization* and we define it as low-intensity urban development that occurs in association with smaller cities (i.e., population <250,000) that spread into surrounding rural areas. The effects of suburban development on landscapes may differ from the effects associated with high-intensity urban development and, therefore, suburbanizaton is of recent interest to scientists, managers, and policy makers (McDonnell and Pickett 1990).

We asked whether suburbanization in the southeastern US could alter physical and biological characteristics of streams historically impaired by agriculture. In general, we predicted that the influence of suburban development on agricultural streams would be similar to, but less intense than, the influence of urban development. We expected streams in watersheds with suburban land use to have flashier hydrographs and greater variation in hydraulic activity than streams in watersheds with agricultural land use. We also expected to find evidence of differences in geomorphology (e.g., channel incision) and erosion dynamics (e.g., suspended and bedload sediment movement) between streams in watersheds with different land uses. We expected substrata in streams in watersheds with suburban development to have a smaller mean size and to have a higher proportion of fine sediments than streams in agricultural watersheds. We predicted that biota sensitive to alterations in hydrology or sedimentation would be less abundant or absent from streams in watersheds with suburban development. Thus, we expected fish and macroinvertebrate assemblages to have lower taxa richness and density, higher proportions of cosmopolitan fishes relative to endemics, and lower diversity of trophic (fish and macroinvertebrates) and reproductive (fish) strategies in streams in watersheds with suburban development than in streams in agricultural watersheds.

Methods

Research watersheds

Suburbanization is occurring in western North Carolina as the city of Asheville sprawls into the surrounding, historically agricultural landscape. We identified potential study sites in 3rd- or 4th-order (1:24,000 scale) streams draining watersheds near Asheville that had agriculture and suburban development. We used the 1993 USGS national land-cover database (NLCD) to quantify the proportion of each watershed in 4 landuse categories: agriculture, urban, forest, and other (Homer et al. 2002, USGS 2002). We verified the presence of agriculture and suburban development by visiting streams. More recent data were unavailable for the study area, but the 1993 data largely confirmed our visual estimates and provided approximations of land use in the study area (Table 1).

We chose 5 sites on streams in watersheds affected by suburban development (suburban sites; Fig. 1).

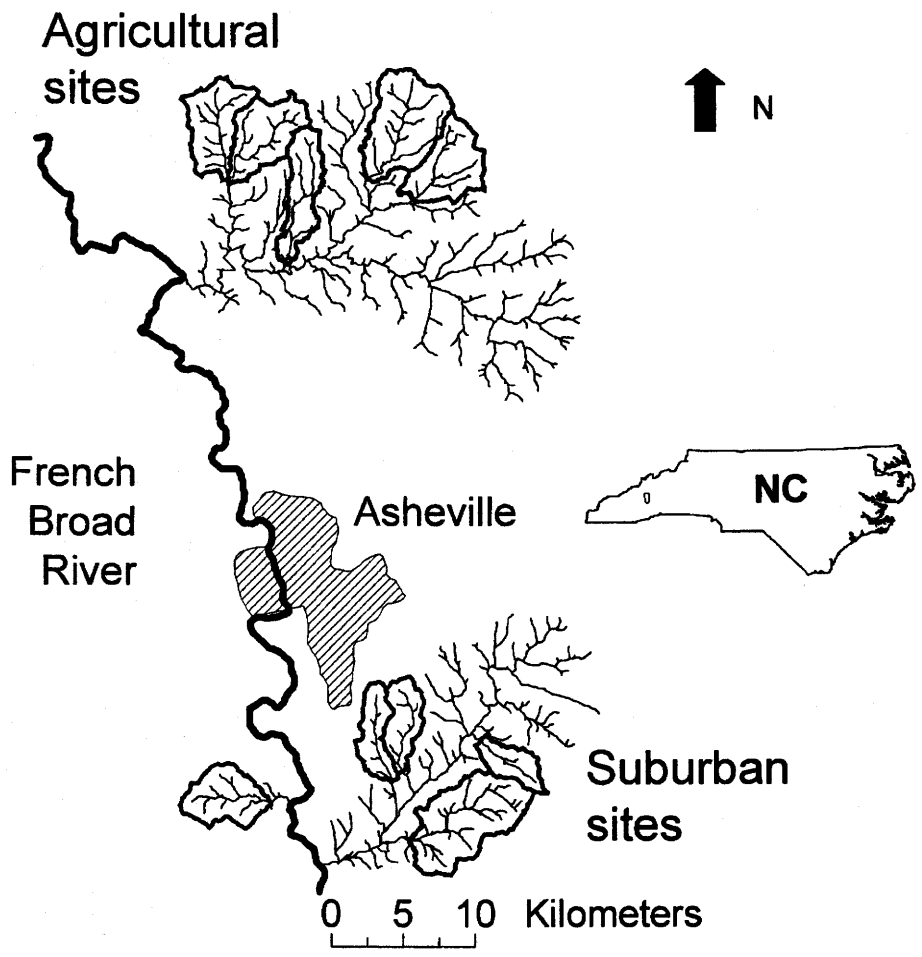

FIG. 1. Study area showing the city of Asheville, the French Broad River, and the study watersheds.

Suitable suburban sites were influenced by past agriculture and recent suburbanization, and these sites were in 3rd- or 4th-order streams. These criteria proved difficult to meet because suburban development was spatially patchy. We were able to identify 5 sites in the French Broad River watershed that had been impaired by historical agriculture but were currently (since ~2000–2001) undergoing residential suburbanization. The 5 suburban sites were compared to 5 sites in similar watersheds that were mostly agricultural and did not have new suburban development (agricultural sites; Fig. 1).

The 10 watersheds were between 987 and 3552 ha ($\bar{x}$ = 1908 ± 257 ha; Table 1) and were similar in geology, soil composition, stream-network development, watershed area, and gradient. We tried to ensure that the major difference among sites was the presence or absence of suburban development in the watershed proximal to stream channels, so there would be a strong likelihood of differences caused by landuse effects.

Physical elements

Hydrologic features.—We identified stream stage height using a TopCon® laser survey unit (Topcon Positioning Systems, Tokyo, Japan) to establish a permanent 0-cm height of baseflow. We measured discharge and recorded stage height approximately monthly for 32 mo at various flows. We developed rating curves describing the relationship between stage height and discharge to estimate discharge beyond the measurable range. We estimated baseflow discharge (stage = 0 cm), stormflow discharge (stage = 50 cm), and the slope of the discharge–stage rating curve (an indication of flashiness [how quickly flow responded to precipitation]) from these data. We used the difference in magnitude between baseflow and stormflow (Qdiff) as a measure of flashiness.

We estimated watershed travel time for rainfall using Hydrologic Engineering Center–Hydrologic Modeling System (HEC–HMS, version 2.0, US Army

Corps of Engineers, Davis, California) equations (Burcher 2005). We used estimates of surface roughness, hill-slope gradient, and proximity to stream channels to calculate the time required for rain to travel between the terrestrial environment and the watershed outlet. We expected surface hydrology to be important to the streams affected by ISC, and we used travel-time estimates to quantify differences in land use (i.e., presence or absence of suburban development). We calculated mean and maximum travel times for each watershed and compared travel times by landuse type.

Geomorphological features.—We measured 3 channel cross-sections (TopCon®) along each 100-m reach periodically in 2002 and 2003 to estimate changes to channel morphology and to metrics derived from cross-sectional data (Montgomery and MacDonald 2002). We calculated bank height, the elevation difference between maximum thalweg depth and floodplain height, for each stream bank, and averaged bank heights as a measure of channel deepening or incision magnitude. We calculated the bank incision ratio, the proportionate angles between maximum thalweg depth and floodplain height, for each bank. We measured bank height and calculated bank incision ratio once during each sampling year and used the difference between years to estimate stream channel movement between sampling dates.

We calculated average baseflow width and depth and the mean width:depth ratio for each stream reach. We used hydrological and geomorphological information to calculate the Froude number as

$$\mathrm{Fr} = \frac{V}{\sqrt{gD}}$$

where V is the mean water velocity (m/s), D is the mean baseflow depth (m), and g is the gravitational constant (m/s^2; from Gordon et al. 2004).

Erosional features.—We estimated 10 erosional metrics from measurements of suspended sediment concentration and bedload composition. We collected suspended sediments using rising-limb sediment samplers (Braatz 1961). We retrieved rising-limb sample bottles after storms and analyzed total suspended solids (TSS) and % fine particulate organic matter (FPOM) using the ash-free-dry-mass (AFDM) method (APHA 1995). We collected bedload samples using 50-cm long, 12-cm diameter polyvinyl chloride (PVC) tubes buried within channels in the stream substrate. These containers collected bedload passively over intervals ranging from ½ to 1 mo. We stored bedload samples in 12-L containers and estimated fine benthic organic matter (FBOM; 0.45 μm < FBOM < 1 mm) from a slurry from the containers to estimate organic and inorganic matter (IM) content of bedload by the AFDM method. We dried and sieved the remaining bedload sample to calculate median particle diameter (D_{50}) and % fine substrates (particles <0.5 mm).

Depositional features.—We estimated benthic substrate characteristics from 3 samples collected once at a riffle–pool interface downstream of a typical riffle in each site. We collected samples with a spade, placed them in a bucket, and air-dried and dry-sieved them. This method effectively sampled only substrate <10 cm and probably greatly underestimated the contribution of fine substrates because some material was lost during collection (Bunte and Abt 2001). However, we assumed that the loss of fine substrate (e.g., sand) associated with the sampling method would be similar among all streams. We created a slurry from wet substrate samples to collect a subsample for AFDM estimation of organic matter content in fine sediments.

Biotic assemblages.—We sampled fishes in August 2002 and 2003 using single-pass backpack electrofishing along 100-m stream reaches. We estimated density ($no./m^2$) as the number of individuals collected/stream area sampled (100 m × mean stream width). We compared density and species composition between 2002 and 2003 and detected no differences between years. Therefore, we considered only the 2002 data in further analyses. We assigned fishes to distribution classes and reproductive and trophic guilds based on available information for each species (Etnier and Starnes 1993, Jenkins and Burkhead 1994, Scott and Helfman 2001).

We collected macroinvertebrates during late April 2003 from 20 quantitative samples (Surber, 500-μm mesh, 0.09 m^2; total area sampled/100-m reach = 1.8 m^2). We estimated density ($no./m^2$) from individual samples and calculated mean density of each taxon for each stream. We preserved macroinvertebrates in 80% ethanol and identified them to the lowest possible taxonomic level (typically genus). We placed taxa in functional feeding groups (FFG) based on Merritt and Cummins (1996) or expert opinion for macroinvertebrates in southern Appalachian streams. We did not consider ontogenetic changes in feeding habits associated with early instars and assumed that individuals of a species could be classified into a single FFG.

Statistical analyses

We measured or estimated 5 hydrological, 10 geomorphological, 6 erosional, 3 depositional (i.e., substrate) elements, and 13 fish and 8 macroinvertebrate metrics at each site (45 variables). We compared sample means between sites in different landuse

TABLE 2. Mean (±1 SE) values of hydrological and geomorphological variables measured at sites in 2 landuse categories. Site codes as in Table 1. Qdiff = difference between baseflow and stormflow discharge estimates, TSS = total suspended solids, D_{50} = median particle diameter. Stormflow discharge occurred at stage = 50 cm. Asterisks (*) denote significant differences between means (*t*-test, $\alpha < 0.05$).

		Landuse category	
Stream response type	Variable	Suburban	Agricultural
Hydrological	Rating curve slope	0.9 (0.1)	0.9 (0.1)
	Baseflow discharge (L/s)	40 (10)	39 (6)
	Stormflow discharge (L/s)	1208 (238)	2163 (1098)
	Qdiff (L/s)	1167 (240)	2123 (1094)
	Mean travel time (min)	178 (30)	113 (39)
	Maximum travel time (min)	559 (91)	797 (325)
Geomorphological	Mean bank height year 1 (m)	1.3 (0.0)	1.3 (0.2)
	Mean bank height year 2 (m)	1.3 (0.0)	1.4 (0.1)
	Mean incision ratio year 1 (%)	33 (3)	30 (3)
	Mean incision ratio year 2 (%)	33 (4)	32 (4)
	Bank height change (m)	0.1 (0.0)	0.2 (0.1)
	Incision ratio change (%)	2 (1)	5 (3)
	Mean baseflow width (m)	3.7 (0.6)	4.5 (0.3)
	Mean baseflow depth (m)	0.14 (0.02)	0.19 (0.02)
	Width:depth ratio	32 (9)	26 (4)
	Froude number	0.14 (0.02)	0.11 (0.02)
Erosional	Mean stormflow TSS (g/L)	*0.20 (0.10)	*1.43 (0.00)
	Mean storm flow TSS organic matter (%)	12 (3)	24 (11)
	Mean storm flow TSS inorganic matter (%)	87 (3)	76 (11)
	Bedload D_{50} (mm)	2.9 (0.4)	2.2 (0.9)
	Bedload fine substrate (%)	32 (4)	36 (2)
	Bedload organic matter (%)	17 (1)	13 (1)
Depositional	Substrate D_{50} (mm)	14.7 (3.5)	17 (3.1)
	Substrate % organic matter (%)	6.8 (0.3)	5.8 (0.2)
	Substrate % fines	13.7 (4.4)	14.2 (4.3)

categories using Student's *t*-tests. Bonferroni adjustment was not necessary because the dependent variable was different for each comparison (e.g., baseflow discharge, particle size, macroinvertebrate taxa richness). We also used multivariate analysis of variance (MANOVA) to detect differences among landuse categories associated with categories of variables (i.e., hydrological, geomorphological, erosional, depositional, or biological metrics). This technique allowed us to consider group-wise variation among intra-elemental variables (e.g., rating-curve slope, mean travel time, etc.) that were present within each variable category. We used MANOVA because it can detect the influence of independent variables (landuse category) on dependent variables (e.g., hydrology) separately or in combination.

We used Detrended Correspondence Analysis (DCA; PCOrd, version 3.18, MjM Software, Glendenen Beach, Oregon) on densities of fish and macroinvertebrates to project sites in the ordination space determined by abiotic or biotic variables to detect small differences in abiotic and biotic responses that might not have been apparent with *t*-tests. DCA projects sites and taxa into the ordination space determined by weighted averages of taxa and site scores (eigenvalues) along ≥1 axes.

Results

Physical responses

Hydrology and geomorphology.—No differences in any hydrological or geomorphological variables were detected between landuse categories with *t*-tests or MANOVA (Table 2). DCA of sites by hydrological and geomorphological variables did not indicate grouping structure or a landuse effect.

Erosional sediment.—Storm-flow TSS differed significantly between sites in different landuse categories (*t*-test, $p < 0.001$), averaging 0.20 ± 0.10 g/L in suburban sites and 1.43 ± 0.0 g/L in agricultural sites (Fig. 2A). However, stormflow TSS data were available for only 4 suburban and 2 agricultural sites because of sample loss during storms. Bedload characteristics were similar between landuse categories (Table 2).

Depositional substrate.—FBOM was significantly higher ($p < 0.05$) in suburban sites (6.8 ± 0.3%) than in agricultural sites (5.8 ± 0.2%; Fig. 2B). Depositional metrics were otherwise similar between landuse

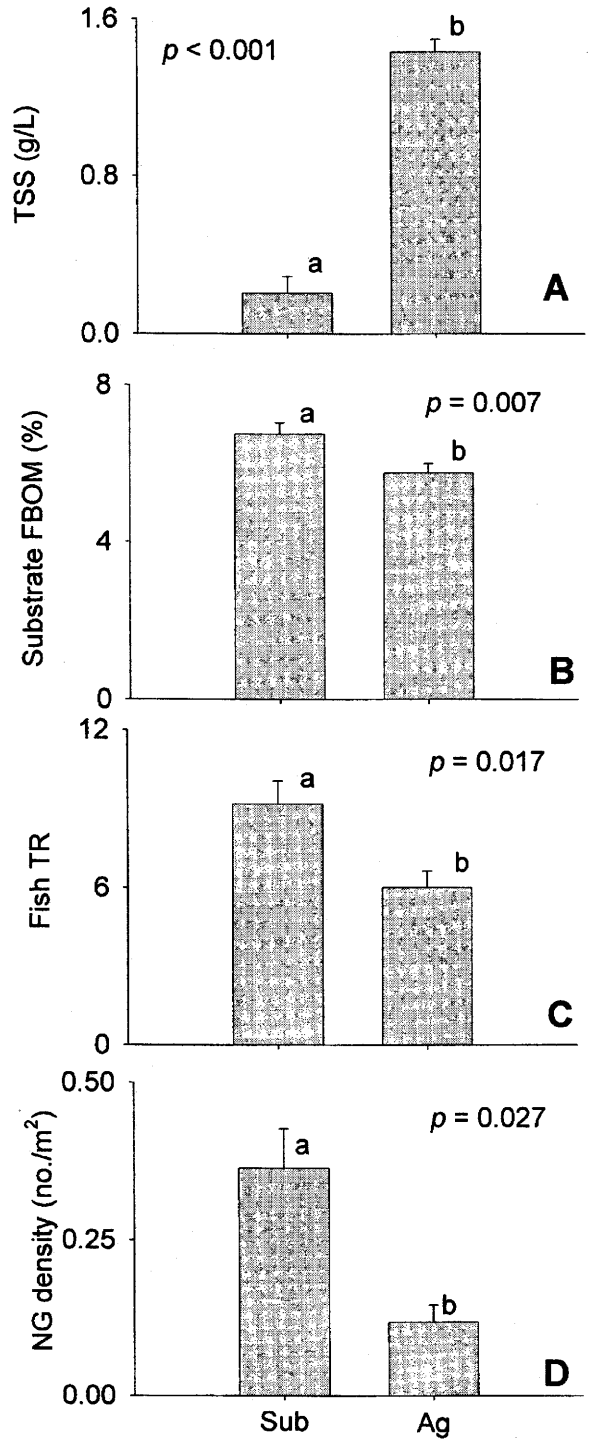

FIG. 2. Mean (+1 SE) stormflow total suspended solids (TSS; A), fine benthic organic matter (FBOM) concentration (B), fish taxa richness (TR; C), and nonguarding (NG) fish density (D) in suburban (Sub) vs agricultural (Ag) sites. Bars with different lower-case letters are significantly different.

categories (Table 2). DCA of sites by substrate attributes did not indicate grouping structure or a landuse effect.

Biotic assemblages

Fish.—We collected 15 fish species (Table 3). Robinson Creek (Sub5, Table 4) had the highest taxa richness of any single site (11 species). In general, fish-assemblage metrics were similar between sites in different landuse categories. Mean total fish density did not differ between landuse categories (suburban: 0.9 ± 0.2/m^2, agricultural: 1.3 ± 0.3/m^2; Table 4). However, fish taxa richness was significantly (p = 0.017) higher in suburban (9 ± 0.9 taxa) than in agricultural (6 ± 0.6 taxa) sites (Fig. 2C). Nonguarding (NG) fish density was significantly (p = 0.007) higher in suburban than in agricultural sites (Fig. 2D). However, cosmopolitan fishes were numerically dominant at sites in both landuse categories. Fish-assemblage trophic structure was dominated by herbivores, and fish-assemblage reproductive structure was dominated by NG species (Fig. 2D) or nest associates (NA) (Table 4).

DCA of sites in fish-species ordination space separated sites on the basis of landuse category (Fig. 3A). Axis 1 (eigenvalue = 0.50) represented a gradient of species density that was driven largely by species absent from sites in one landuse category but present at sites in the other landuse category (e.g., redbreast sunfish were present only in suburban sites). Little variation existed on axis 2 (eigenvalue = 0.04). Thus, most of the variation in assemblage structure could be explained by the occurrence and relative density of individual taxa. Suburban-site assemblages were dominated by cyprinids including warpaint shiners, blacknose dace, and saffron shiners; centrarchids including bluegill, redbreast sunfish, and rock bass; and mountain brook lamprey (Fig. 3A). Agricultural-site assemblages were dominated by northern hog-suckers, fantail darters, and whitetail shiners.

Macroinvertebrates.—Macroinvertebrate assemblage metrics did not differ significantly between landuse categories (Table 5). Mean taxa richness was 11 ± 2 for all sites. Mean total macroinvertebrate densities were 654 ± 202/m^2 in agricultural and 700 ± 199/m^2 in suburban sites. Chironomids made up 19 to 33% of invertebrate densities in agricultural and suburban sites, respectively (suburban: 230 ± 57/m^2, agricultural: 121 ± 35/m^2). Shredders were nearly absent from agricultural sites (2 ± 2/m^2), but averaged 19 ± 11/m^2 in suburban sites. Macroinvertebrate assemblages in sites in both landuse categories were dominated by scrapers or collector-gatherers. Scrapers

TABLE 3. Mean (±1 SE) fish density by site landuse category and fish guild-assignment categories. Distribution status: Cos = cosmopolitan or widely distributed, End = endemic to local drainages, N = neither cos nor end. Reproductive guild: NB = nest builder, guarder, NA = nest associate, NG = burying nonguarder, BC = broadcast spawner. Trophic guild: Herb = herbivore, BI = benthic invertivore, GI = general invertivore, DI = drift invertivore, D = detritivore.

Common name[a]	Density (no./m²)		Distribution status	Reproductive guild	Trophic guild
	Suburban	Agricultural			
Creek chub	0.288 (0.05)	0.04 (0.02)	Cos	NG	GI
Blacknose dace	0.17 (0.04)	0.22 (0.05)	Cos	BC	Herb
Northern hogsucker	0.03 (0.01)	0.08 (0.02)	Cos	NG	BI
Bluegill sunfish	0.08 (0.03)	0.002 (0.002)	Cos	NB	Herb
Central stoneroller	0.10 (0.07)	0.74 (0.31)	Cos	NA	GI
Warpaint shiner	0.06 (0.05)	0.03 (0.02)	End	NA	DI
White sucker	0.02 (0.00)	0.01 (0.01)	Cos	BC	D
Mottled sculpin	0.06 (0.03)	0	End	NB	BI
Fantail darter	0.03 (0.01)	0.22 (0.08)	N	NB	BI
Mountain brook lamprey	0.02 (0.00)	0	Cos	NG	D
Rock bass	0.002 (0.002)	0	Cos	NB	GI
Saffron shiner	0.03 (0.02)	0	End	NG	DI
Redbreast sunfish	0.002 (0.002)	0	Cos	NB	Herb
Whitetail shiner	0	0.004 (0.004)	N	NA	Herb
Rainbow trout	0	0.002 (0.002)	N	NG	GI

[a] See Appendix 1 for species names

made up 23 to 29% of invertebrate densities in agricultural and suburban sites, respectively (suburban: 205 ± 60/m², agricultural: 151 ± 82/m²), whereas collector-gatherers made up 20 to 37% of invertebrate densities in suburban and agricultural sites, respectively (suburban: 138 ± 59/m², agricultural: 245 ± 89/m²). Collector-filters made up 3 to 37% of invertebrate density in suburban sites (60 ± 22/m²) and 4 to 12% in agricultural sites (121 ± 25/m²). Predators made up 7% of invertebrate density in suburban sites (47 ± 17/m²) and only 2% in agricultural sites (15 ± 8/m²).

DCA of sites in macroinvertebrate-taxon ordination space separated sites by landuse category (Fig. 3B). Similar to DCA by fish species, Axis 1 (eigenvalue = 0.48) represented a gradient of taxa density that was driven largely by taxa absent in one landuse type but present in the other. Axes 2 and 3 did not add explanatory value to axis 1 and were not interpreted. Macroinvertebrate assemblages in suburban sites were dominated by dipterans, mostly chironomids. Agricultural sites also had high chironomid densities, but were dominated by the ephemeropterans of the genera *Ephemerella*, *Stenonema*, and *Epeorus*. Many taxa

TABLE 4. Fish taxa richness, total density, and density calculated by distribution status, trophic guild, and reproductive guild in the study sites. Site codes and abbreviations as in Tables 1 and 3. Asterisks (*) denote significant effect of landuse category at $\alpha < 0.05$.

Stream	Taxa richness*	Total density (no./m²)	Distributional status		Trophic guild					Reproductive guild			
			Cos	End	Herb	BI	GI	DI	Det	NB	NA	NG*	BC
Sub1	10	0.9	0.6	0.3	0.3	0.2	0.2	0.2	0.1	0.2	0.3	0.2	0.2
Sub2	9	0.7	1.2	0.1	0.2	0.1	0.3	0.0	0.0	0.1	0.1	0.3	0.1
Sub3	10	1.3	0.9	0.2	0.4	0.2	0.2	0.2	0.1	0.1	0.4	0.5	0.4
Sub4	6	0.5	0.4	0.0	0.1	0.3	0.5	0.0	0.0	0.1	0.0	0.3	0.1
Sub5	11	1.2	0.6	0.1	0.3	0.0	0.7	0.1	0.1	0.5	0.0	0.5	0.2
Ag1	5	0.6	1.3	0.1	0.3	0.1	1.8	0.0	0.0	0.3	0.0	0.0	0.3
Ag2	4	2.3	0.9	0.1	0.4	0.3	0.6	0.1	0.0	0.0	1.8	0.1	0.4
Ag3	7	1.1	2.3	0	0.1	0.1	0.2	0.2	0.0	0.2	0.6	0.2	0.1
Ag4	7	1.9	0.4	0	0.1	0.0	0.2	0.0	0.2	0.5	1.1	0.2	0.1
Ag5	7	0.9	0.7	0	0.3	0.3	0.0	0.0	0.0	0.2	0.3	0.1	0.3
Mean (±1 SE) Sub	9*	0.9	0.7	0.2	0.3	0.2	0.4	0.1	0.0	0.2	0.2	0.4*	0.2
	(0.9)	(0.2)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.0)	(0.1)	(0.1)	(0.1)	(0.1)
Mean (±1 SE) Ag	6*	1.3	1.1	0.1	0.2	0.1	0.6	0.1	0.0	0.2	0.8	0.1*	0.2
	(0.6)	(0.3)	(0.3)	(0.0)	(0.1)	(0.1)	(0.3)	(0.0)	(0.1)	(0.1)	(0.3)	(0.0)	(0.1)

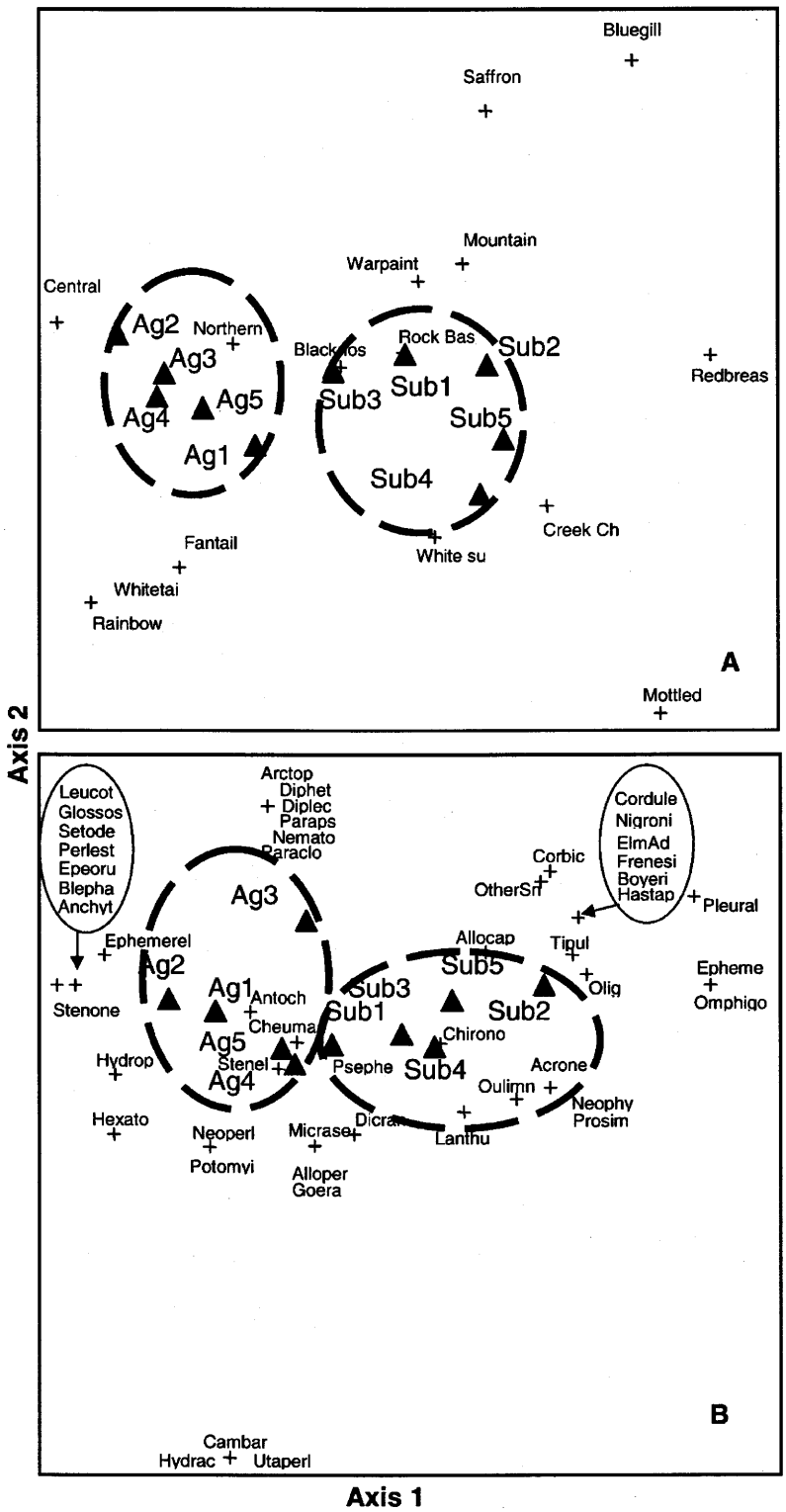

FIG. 3. Detrended Correspondence Analysis of streams by fish (A) and macroinvertebrate (B) density. Triangles indicate locations of streams in the hypothetical space defined by species distribution. Dashed circles indicate grouping of sites by landuse category (agriculture [Ag] and suburban [Sub]). Circles group macroinvertebrate taxa common to one ordination location and are based on maximum eigenvalue distance. Fish common names are truncated to 8 letter abbreviations and can be found in Appendix 1. Macroinvertebrate names (genera and family) are truncated to 8 letter abbreviations and can be found in Appendix 2.

TABLE 5. Macroinvertebrate taxa richness, total density, and density calculated by functional feeding group in the study sites. Site codes as in Table 1. TR = taxa richness, SH = shredder, SC = scraper, CG = collector-gatherer, CF = collector-filterer, P = predator.

	Taxonomic			Functional feeding group				
Stream	TR	Density	Midge	SH	SC	CG	CF	P
Sub1	14	883	183	11	248	291	54	97
Sub2	8	452	172	0	161	75	22	22
Sub3	5	161	108	11	11	22	11	0
Sub4	13	667	248	11	226	32	86	65
Sub5	13	1335	441	65	377	269	129	54
Ag1	15	1421	248	11	474	538	108	43
Ag2	5	635	65	0	43	366	161	0
Ag3	13	420	54	0	108	129	129	0
Ag4	11	258	97	0	32	75	32	22
Ag5	10	538	140	0	97	118	0.1	11
Mean (±1 SE) Sub	11 (2)	700 (199)	230 (57)	19 (11)	205 (60)	138 (59)	60 (22)	47 (17)
Mean (±1 SE) Ag	11 (2)	654 (202)	121 (35)	2 (2)	151 (82)	245 (89)	121 (25)	15 (8)

occurred at sites in only one landuse category, but 9 taxa (largely made up of chironomids, pleurocerid snails, ephemerellid mayflies, *Psephenus* and *Stenelmis* (Coleoptera), tipulids, and hydropsychid caddisflies) were present at sites in both landuse categories.

Discussion

In general, streams draining historically agricultural watersheds presently undergoing suburbanization were not significantly different from streams draining agricultural watersheds not undergoing development. No major hydrological or geomorphological differences were apparent between sites in the 2 landuse categories, although stormflow TSS was lower and substrate FPOM was higher in suburban than in agricultural sites. Macroinvertebrate assemblages did not differ significantly between sites in the 2 landuse categories, but total and NG fish density were higher in suburban than in agricultural sites. Nevertheless, sites could be grouped by landuse categories in ordinations based on both fish and macroinvertebrate assemblage compositions, suggesting that subtle differences were present between assemblages in the 2 landuse categories, even though differences in individual taxa or metrics usually could not be detected with *t*-tests or MANOVA. This evidence suggests that suburbanization induces subtle, rather than dramatic, changes in erosion, organic matter dynamics, and assemblage structure in watersheds.

Physical responses

TSS.—We expected TSS to increase with suburbanization. However, TSS concentration was significantly lower ($p < 0.001$) in suburban sites than in agricultural sites (Fig. 2A). We attribute this unexpected result to sequential changes in overland flow and channel hydrology in suburban sites. During the initial phase of urbanization, watersheds contribute suspended sediments associated with construction to streamflow but, later in urbanization, suspended sediment loads decrease relative to predisturbance conditions (Finkenbine et al. 2000). Low TSS concentrations in the suburban sites in our study could indicate that these sites were no longer receiving sediments associated with the initial phases of construction. However, this explanation implies that some hydrological element interacts with sediments, and we did not detect an effect of suburbanization on the hydrological elements we quantified. Nevertheless, some unmeasured hydrological effect (e.g., streambed shear stress [Krishnappan 2004] or terrestrial erosion) must have been influencing TSS.

We suggest that surface runoff may have been more erosional in agricultural watersheds, delivering more suspended material to stream channels than surface runoff in suburban watersheds. Moreover, runoff in suburban watersheds may have been exposed to a smaller volume of soil than runoff in agricultural watersheds. Suburban landscapes tend to have greater ISC than agricultural landscapes, and ISC reduces the erosional potential of land surfaces (Jennings and Jarnagin 2002) and reduces suspended particulate loads in runoff (Booth 1990, Crosbie and Chow-Frasier 1999). Suburban sites probably carried a lower TSS load than agricultural sites because of more ISC and less instream particulate resuspension. Instream sediment resuspension also contributes to TSS concentration, and it is uncertain whether higher TSS in agricultural sites was caused by near-stream erosion, instream resuspension, or bank failure (Owens and Walling 2002).

FBOM.—Percent FBOM was significantly higher in suburban sites than in agricultural sites (Fig. 2B). This

result suggests that the IM fraction of the substrate was lower in suburban sites than in agricultural sites, an interesting result considering that TSS levels also were lower in suburban sites than in agricultural sites. Taken together, TSS and IM information suggests that streams draining agricultural watersheds were more erosional in the terrestrial environment (indicated by higher TSS) and disturbed instream substrate more than streams draining suburban watersheds. Retention mechanisms may have differed with landuse category (Wang et al. 2001), but we did not quantify these features.

Our inability to detect significant differences in hydrological variables may have been a result of the high variances associated with these measures (Table 2) and the difficulty of quantifying them. Hydrological elements are notoriously difficult to quantify because of the stochastic nature of storms (Wondzell and Swanson 1999, Lake 2000), variability between high-flow periods (Resh et al. 1988), and long-term hydrological patterns (Richter et al. 1992).

Some hydrological differences between landuse types were apparent but were not statistically different. For example, the difference between baseflow and stormflow (Qdiff) averaged 1167 ± 240 L/s in suburban sites and 2123 ± 1094 L/s in agricultural sites. This difference represents a discharge increase of 1 to 2 orders of magnitude for streams that averaged 40 L/s during typical baseflow condition. In general, all study streams appeared extremely flashy (CLB, personal observation), an observation that was supported by USGS stream gages located on the mainstem Ivy Creek and near the confluence of Cane Creek on the mainstem French Broad River (http://waterdata.usgs.gov/nwis/rt). We did not quantify flood recurrence interval, and we have no historic record documenting floods in these streams, but we observed several storms during the study period that would be considered catastrophic (i.e., streams breached 100-y floodplain stage multiple times during a single year) and stormflows recorded by nearby USGS gages during this period (March and April 2002 and 2003) were exceptionally high. If stream channels had been influenced previously by such flows, further geomorphological changes probably would have been induced only by catastrophic flows beyond these observed during our study (Paul and Meyer 2001).

Fish-assemblage responses

DCA clearly indicated that fish assemblages differed between landuse categories, and we attribute this difference to differences in hydrology and sediment dynamics. An alternative explanation for the difference is the nested condition of sites within parent watersheds (e.g., agricultural sites all drained into Ivy Creek, suburban sites all were tributaries of Cane Creek). However, mainstem streams were in close geographical proximity (~50 km) to each other and were joined by the French Broad River, so movement of fish between watersheds probably was not inhibited. If we assume that the likelihood of a taxon being present was similar for sites in both landuse categories, then the presence of suburbanization near sites is a strong explanation of observed taxonomic differences because DCA arranged sites into 2 nonoverlapping groups, and those groups corresponded with our a priori classification of suburban or agricultural sites.

The reproductive ecology of fish assemblages differed between sites in different landuse categories. Redbreast, bluegill, and rock bass sunfishes were present in suburban sites, whereas these centrarchids were absent from agricultural sites. Mottled sculpin were present in 4 of 5 suburban sites, but were absent from agricultural sites. We suggest that the higher density of nonguarding (NG) fishes in suburban than in agricultural sites probably was a result of the ability of centrarchids and sculpin to clean substrata for nests or of their tolerance of the hydrologic regime present in suburban sites. Nest builders (NB) were poorly represented in agricultural sites, possibly because of higher loads of inorganic sediments in substrata in agricultural sites. Nest associates (NA; mostly the cyprinid central stonerollers and whitetail shiners) dominated agricultural sites. These 2 species typically spawn in association with aggregations of NBs (e.g., creek chub) but can spawn successfully in the absence of nests (Jenkins and Burkhead 1994). The only NBs encountered in agricultural streams were bluegill and the percid fantail darter, and we assumed that cyprinid NAs were spawning by alternative methods in agricultural sites (Etnier and Starnes 1993).

We collected 3 fish species (warpaint and saffron shiners and mottled sculpin) endemic to highland streams during our study. Of these, only warpaint shiners were collected in agricultural sites. The lower representation of endemic species in agricultural sites could have reflected higher relative availability of diverse habitat and trophic resources in suburban sites than in agricultural sites. Sculpin rely on benthic interstices for feeding and reproduction, and their absence from agricultural streams could be related to the increased inorganic sedimentation we observed in agricultural sites.

Macroinvertebrate-assemblage responses

Total density of macroinvertebrates was similar between landuse categories, but DCA based on taxonomic composition indicated that macroinvertebrate assemblages differed between landuse categories

(Fig. 3B). Shredders and scrapers were dominant in suburban sites (73% of nonchironomid taxa), whereas collector-gatherers and collector-filterers were dominant in agricultural sites (69% of nonchironomid taxa). We attribute higher scraper density in suburban sites than in agricultural sites to lower IM associated with the substrata in suburban sites. Scrapers depend on benthic algae, and scouring or filling associated with fine IM may have decreased the suitability of substrata for algal production in agricultural sites (Sutherland et al. 2002, Matthaei et al. 2003). Stream banks along suburban sites often were vegetated to some degree, whereas agricultural-site stream banks were nearly always denuded. Higher collector-filterer density in agricultural sites than in suburban sites was largely attributable to hydropsychid caddisflies that filter particulate organic matter from the water column using silk nets located on rock surfaces. Collector-gatherers rely on motility to locate and collect organic matter and largely consisted of *Ephemerella* and *Epeorus* in agricultural sites. In contrast, hydropsychid caddisflies and *Ephemerella* were much less abundant and *Epeorus* was absent in suburban sites.

Influence of suburbanization

Though subtle, the differences between landuse categories suggest a relationship between assemblage structure, sediment dynamics, and hydrology. Fish assemblages influenced by suburbanization had more endemic species, more centrarchids, more mottled sculpin, and more NG fish species than assemblages in agricultural sites. Invertebrate assemblages influenced by suburbanization included taxa that fed largely on algae and leaves, whereas invertebrate assemblages in agricultural streams probably depended more on transported detritus. These differences suggest that suburbanization did change landscapes (probably because of increased ISC), but the influence of these changes on historically agricultural streams was smaller than expected. We see at least 2 explanations for our inability to detect major differences between assemblages in sites in different landuse categories: 1) The intensity of suburbanization ($\ll$10–12% in our study) may not have been great enough to induce a measurable effect, or insufficient time may have elapsed for the streams to respond to this level of disturbance. This possibility is supported by the urban literature that suggests that a threshold of 10 to 12% ISC is necessary to induce detrimental changes in streams draining urban watersheds (e.g., Wang et al. 2001, Booth 2005). 2) The intensity of agriculture in the study area may have overwhelmed the influence of suburbanization. In other words, streams were already very disturbed and responded only subtly to further perturbation. Harding et al. (1998) suggested that agricultural streams in western North Carolina may continue to show agricultural influences for long periods of time after agriculture ceases. Thus, the influence of suburbanization on stream ecosystems probably will depend on the intensity and duration of suburbanization coupled with the history of land use in the watershed. Investigations in such systems should consider using multiple approaches to detect subtle differences that might not be apparent with inferential statistics.

Acknowledgements

This research was supported by the National Science Foundation grant DEB-9632854 to the Virginia Tech Coweeta LTER. We thank P. L. Angermeier, J. R. Voshell, J. R. Webster, and R. H. Wynne for comments on earlier drafts.

APPENDIX 1. Fish taxa collected in suburban and agricultural streams. Abbreviations are truncated common names.

Family	Scientific name	Common name	Abbreviation
Petromyzontidae	*Ichthyomyzon greeleyi*	Mountain brook lamprey	Mountain
Cyprinidae	*Campostoma anomalum*	Central stoneroller	Central
	Cyprinella galactura	Whitetail shiner	Whitetai
	Luxilus coccogenis	Warpaint shiner	Warpaint
	Notropis rubricroceus	Saffron shiner	Saffron
	Rhinichthys atratulus	Eastern blacknose dace	Blacknos
	Semotilus atromaculatus	Creek chub	Creek Ch
Catostomidae	*Catostomus commersonii*	White sucker	White su
	Hypentelium nigricans	Northern hogsucker	Northern
Salmonidae	*Oncorhynchus mykiss*	Rainbow trout	Rainbow
Cottidae	*Cottus baridii*	Mottled sculpin	Mottled
Centrarchidae	*Ambloplites rupestris*	Rock bass	Rock Bas
	Lepomis auritus	Redbreast sunfish	Redbreas
	Lepomis macrochirus	Bluegill sunfish	Bluegill
Percidae	*Etheostoma flabellare*	Fantail darter	Fantail

APPENDIX 2. Macroinvertebrate taxa collected in suburban and agricultural streams. Abbreviations are truncated taxa names.

Order	Family	Genera	Abbreviation
Nematoda	–	–	Nemato
Annelida	Oligochaeta	–	Olig
Lumbriculida	Lumbriculidae	*Lumbriculus*	Lumbric
Decapoda	Cambaridae	*Cambarus*	Cambar
Plecoptera	Capniidae	*Allocapnia*	Allocap
	Chloroperlidae	*Alloperla*	Alloper
		Hastaperla	Hastap
		Utaperla	Utaperl
	Perlidae	*Acroneuria*	Acrone
		Neoperla	Neoperl
		Perlesta	Perlest
Ephemeroptera	Baetidae	*Diphetor*	Diphet
		Paracloeodes	Paraclo
	Ephemeridae	*Ephemera*	Epheme
	Ephemerellidae	*Ephemerella*	Ephemerel
	Heptageniidae	*Epeorus*	Epeoru
		Stenonema	Stenone
Odonata	Aeshnidae	*Boyeria*	Boyeri
	Cordulegasteridae	*Cordulegaster*	Cordule
	Gomphidae	*Lanthus*	Lanthu
		Ophiogomphus	Omphigo
Megaloptera	Corydalidae	*Nigronia*	Nigroni
Trichoptera	Brachycentridae	*Micrasema*	Micrase
	Glossosomatidae	*Glossosoma*	Glossos
	Goeridae	*Goera*	Goera
	Hydropsychidae	*Arctopsyche*	Arctop
		Cheumatopsyche	Cheuma
		Diplectrona	Diplec
		Hydropsyche	Hydrop
		Parapsyche	Paraps
		Potomyia	Potomy
	Hydroptilidae	*Leucotrichia*	Leucot
	Leptoceridae	*Setodes*	Setode
	Limnephilidae	*Frenesia*	Frenesi
	Uenoidae	*Neophylax*	Neophy
Coleoptera	Elmidae	Elmid adult	ElmAd
		Oulimnus	Oulimn
		Stenelmis	Stenel
Coleoptera	Psephenidae	*Psephenus*	Psephe
	Ptilodactylidae	*Anchytarsus*	Anchyt
Diptera	Blephariceridae	*Blepharicera*	Blepha
	Chironomidae	–	Chirono
	Tabanidae	*Tabanus*	Tabanu
Diptera	Simuliidae	*Prosimulium*	Prosim
	Tipulidae	*Antocha*	Antoch
		Dicranota	Dicran
		Hexatoma	Hexato
		Tipula	Tipula
Hydracarina	–	–	Hydrac
Gastropoda	Pleuroceridae	*Pleurocera*	Pleural
	–	–	OtherSn (other snails)
Unionidea	Corbiculidae	*Corbicula*	Corbic

Literature Cited

APHA (AMERICAN PUBLIC HEALTH ASSOCIATION). 1995. Standard methods for the examination of water and wastewater. 19th edition. American Public Health Association, American Waterworks Association, and Water Environment Federation, Washington, DC.

BHADURI, B., J. HARBOR, B. ENGEL, AND M. GROVE. 2000. Assessing watershed-scale, long-term hydrologic impacts of land use change using a GIS-NPS model. Environmental Management 26:643–658.

BOOTH, D. B. 1990. Stream channel incision following drainage basin urbanization. Water Resources Bulletin 26:407–417.

BOOTH, D. B. 2005. Challenges and prospects for restoring urban streams: a perspective from the Pacific Northwest of North America. Journal of the North American Benthological Society 24:724–737.

BRAATZ, D. A. 1961. The single-stage sampler for suspended sediment. Subcommittee on Sedimentation, Inter-Agency Committee on Water Resources Report No. 13. St. Anthony Falls Hydraulic Laboratory, Minneapolis, Minnesota. (Available from: St. Anthony Falls Laboratory, Mississippi River at 3rd Avenue SE, Minneapolis, Minnesota 55414 USA.)

BUNTE, K., AND S. R. ABT. 2001. Sampling surface and subsurface particle-size distributions in wadable gravel- and cobble-bed streams for analyses in sediment transport, hydrology, and streambed monitoring. General Technical Report RMRS-GTR-74. Rocky Mountain Research Station, Forest Service, US Department of Agriculture, Fort Collins, Colorado.

BURCHER, C. L. 2005. Biotic and abiotic responses to rural development and legacy agriculture by southern Appalachian streams. PhD Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

CROSBIE, B., AND P. CHOW-FRASER. 1999. Percentage land use in the watershed determines the water and sediment quality of 22 marshes in the Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences 56:1781–1791.

CUFFNEY, T. F., M. R. MEADOR, S. D. PORTER, AND M. E. GURTZ. 2000. Responses of physical, chemical and biological indicators of water quality to a gradient of agricultural land use in the Yakima River basin, Washington. Environmental Monitoring and Assessment 64:259–270.

ETNIER, D. A., AND W. C. STARNES. 1993. The fishes of Tennessee. University of Tennessee Press, Knoxville, Tennessee.

FINKENBINE, J. K., J. W. ATWATER, AND D. S. MAVINIC. 2000. Stream health after urbanization. Journal of the American Water Resources Association 5:1149–1160.

GORDON, N. D., T. A. MCMAHON, B. L. FINLAYSON, C. J. GIPPEL, AND R. J. NATHAN. 2004. Stream hydrology: an introduction for ecologists. 2nd edition. John Wiley and Sons, Hoboken, New Jersey.

HARDING, J. S., E. F. BENFIELD, P. V. BOLSTAD, G. S. HELFMAN, AND E. B. D. JONES. 1998. Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Science of the United States of America 95:14843–14847.

HEIMLICH, R. E., AND W. D. ANDERSON. 2001. Development at the urban fringe and beyond: impacts on agriculture and rural land. USDA Agricultural Economic Report 803. Economic Research Service, US Department of Agriculture, Washington, DC.

HOMER, C. G., C. HUANG, L. YANG, AND B. WYLIE. 2002. Development of a circa 2000 landcover database for the United States. American Society of Photogrammetry and Remote Sensing Proceedings, April 2002. American Society of Photogrammetry and Remote Sensing, Washington, DC. (Available from: http://landcover.usgs.gov)

HUNTER, L. M. 2000. The environmental implications of population dynamics. RAND monograph report MR-1191-WFHF/RF/DLPF. The RAND Corporation, Santa Monica, California. (Available from: The RAND Corporation, 1776 Main St., P.O. Box 2138, Santa Monica, California 90407-2138 USA.)

JENKINS, R. E., AND N. M. BURKHEAD. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

JENNINGS, D. B., AND S. T. JARNAGIN. 2002. Changes in anthropogenic impervious surfaces, precipitation and daily streamflow discharge: a historical perspective in a mid-Atlantic subwatershed. Landscape Ecology 17:471–489.

JONES, J. A., F. J. SWANSON, B. C. WEMPLE, AND K. U. SNYDER. 2000. Effects of roads on hydrology, geomorphology and disturbance patches in stream networks. Conservation Biology 14:76–85.

KRISHNAPPAN, B. G. 2004. Erosion behavior of fine sediment deposits. Canadian Journal of Civil Engineering 31:759–766.

LAKE, P. S. 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19:573–592.

MATTHAEI, C. D., C. GUGGELBERGER, AND H. HUBER. 2003. Local disturbance history affects patchiness of benthic river algae. Freshwater Biology 48:1514–1526.

MCDONNELL, M. J., AND S. T. A. PICKETT. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology 71:1232–1237.

MERRITT, R. W., AND K. W. CUMMINS (EDITORS). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

MEYER, W. B., AND B. L. TURNER. 1992. Human population growth and global land use/cover change. Annual Review of Ecology and Systematics 23:39–61.

MONTGOMERY, D. R., AND L. H. MACDONALD. 2002. Diagnostic approach to stream channel assessment and monitoring. Journal of the American Water Resources Association 38: 1–16.

NELLER, R. J. 1988. A comparison of channel erosion in small urban and rural catchments, Armidale, New South Wales. Earth Surface Processes and Landforms 13:1–7.

OWENS, P. N., AND D. E. WALLING. 2002. Changes in sediment sources and floodplain deposition rates in the catchment of the river Tweed, Scotland, over the last 100 years: the impact of climate and land use change. Earth Surface Processes and Landforms 27:403–423.

PAUL, M. J., AND J. L. MEYER. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333–365.

POFF, N. L., AND J. D. ALLAN. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76:606–627.

RAMANKUTTY, N., J. A. FOLEY, AND N. J. OLEJNICZAK. 2002. People on the land: changes in global population and croplands during the 20th century. Ambio 31:251–257.

RESH, V. H., A. V. BROWN, A. P. COVICH, M. E. GURTZ, H. W. LI, G. W. MINSHALL, S. R. REICE, A. L. SHELDON, J. B. WALLACE, AND R. C. WISSMAR. 1988. The role of disturbance in

stream ecology. Journal of the North American Benthological Society 7:433–455.

RHOADS, B. L., AND R. A CAHILL. 1999. Geomorphological assessment of sediment contamination in an urban stream system. Applied Geochemistry 14:459–483.

RICHTER, B. D., J. V. BAUMGARTNER, J. POWELL, AND D. P. BRAUN. 1992. A method for assessing hydrologic alteration within ecosystems. Conservation Biology 4:1163–1174.

ROY, A. H., M. C. FREEMAN, B. J. FREEMAN, S. J. WENGER, W. E. ENSIGN, AND J. L. MEYER. 2005. Investigating hydrological alteration as a mechanism of fish assemblage shifts in urbanizing streams. Journal of the North American Benthological Society 24:656–678.

SCOTT, M. C., AND G. S. HELFMAN. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26(11):6–15.

STANLEY, E. H., M. A. LUEBKE, M. W. DOYLE, AND D. W. MARSHALL. 2002. Short-term changes in channel form and macroinvertebrate communities following low-head dam removal. Journal of the North American Benthological Society 21:172–187.

SUTHERLAND, A. B., J. L. MEYER, AND E. P. GARDINER. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. Freshwater Biology 47:1791–1805.

SWANK, W. T., J. M. VOSE, AND K. J. ELLIOTT. 2001. Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalachian catchment. Forest Ecology and Management 143:168–178.

TRIMBLE, S. W. 1997. Contribution of stream channel erosion to sediment yield from an urbanizing watershed. Science 278:1442–1444.

UNITED NATIONS. 1999. World Urbanization Project: the 1999 revision. Population Division, Department of Economic and Social Affairs, United Nations, New York. (Available from: http://www.un.org/esa/population/publications/wup1999/wup99.htm)

USGS (US GEOLOGICAL SURVEY). 2002. Multi-Resolution Land Characteristics (MRLC) Consortium land-cover dataset. US Geological Survey, US Department of the Interior, Washington, DC. (Available from: http://www.seamless.gov)

WANG, L., J. LYONS, P. KANEHL, AND R. BANNERMAN. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28:255–266.

WEAR, D. N., M. G. TURNER, AND R. J. NAIMAN. 1998. Land cover along an urban-rural gradient: implications for water quality. Ecological Applications 8:619–630.

WONDZELL, S. M., AND F. J. SWANSON. 1999. Floods, channel change, and the hyporheic zone. Water Resources Research 35:555–567.

Received: 19 May 2005
Accepted: 30 December 2005