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Habitat-specific responses of stream insects to land cover disturbance: biological consequences and monitoring implications

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Abstract. Changes in catchment land cover can impact stream ecosystems through altered hydrology and subsequent increases in sedimentation and nonpoint-source pollutants. These stressors can affect habitat suitability and water quality for aquatic invertebrates. We studied the impact of a range of physical and chemical stressors on aquatic insects, and tested whether the effects of these stressors differed in 3 habitat types: riffles, pools, and banks. Our study was conducted in Piedmont streams in Georgia (USA) where catchment development pressure and the potential for aquatic biodiversity loss are high. We sampled 3 replicates of riffle, pool, and bank habitats within a 100-m reach of 29 streams (11–126 km²) that varied in catchment land cover. Correlations between environmental variables and aquatic insects (both richness and density) within habitat types indicated that riffle habitats (vs pool and bank habitats) exhibited the strongest relations with environmental variables. Riffle assemblages were negatively affected by both physical (e.g., bed mobility) and chemical (e.g., specific conductance, nutrient concentrations) variables. The density of aquatic insects in pools was also correlated to physical and chemical variables, but there were few relationships with pool or bank richness or bank density. Because of greater relative impacts of disturbance in riffles versus banks, we found greater differences between riffle and bank richness in streams with greater sediment disturbance. The proportion of bank richness (bank richness/bank + riffle richness) increased with finer bed sediment ($r^2 = 0.43$) and increased bed mobility ($r^2 = 0.35$). We compared richness of facultative taxa (found in multiple habitats) between sites we characterized as minimally impacted and sediment-impacted. In riffles, richness of facultative taxa was lower in sediment-impacted vs minimally impacted sites (11.0 vs 20.2, $p = 0.002$, t -test), but was similar for both disturbance groups in banks (20.1 vs 22.7, $p > 0.05$, t -test). Our results suggest that taxa richness may be retained in bank habitats when riffle quality is poor and banks may serve as a refuge in highly disturbed systems. Such shifts in the distribution of benthos may be an early warning indicator of biotic impairment and have implications for biomonitoring and maintenance of habitat.

Key words: stream, macroinvertebrates, insects, urbanization, sedimentation, land use, habitat, refuge, water quality, disturbance, biomonitoring, Piedmont, southeastern United States.

Landscapes are changing at an unprecedented rate because of increases in urban land cover and additional changes in forested and agricultural land cover (USDA 2000). These changes impact stream biotic integrity (Jones and Clark 1987, Wang et al. 1997) through altered chemistry (Klein 1979, Herlihy et al. 1998), increased sedimentation, and longer-term changes in geomorphology (Waters 1995, Trimble 1997). In Piedmont streams, a primary threat of land cover disturbance is mobilization of fine sediment from the landscape and within the stream chan-

nel (Wood and Armitage 1997). Sediment storage and remobilization is commonly thought to be a result of past agricultural practices (Harding et al. 1998), increases in impervious surfaces (Meade et al. 1990, Trimble 1997), and/or reduced riparian forest cover (Waters 1995). In addition, urbanization contributes to excessive sediment yield in streams, particularly from construction sites (Wolman and Schnick 1967). Increased sedimentation can affect aquatic insects by reducing habitat or making the habitat unsuitable for organisms to survive (see review by Wood and Armitage 1997). Small particles deposited in riffles can fill interstices between larger particles where invertebrates live and feed (Richards and Bacon 1994). This reduction in desirable habitat may result in decreased

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density and diversity (Waters 1995), and/or secondary production of insects (Lamberti and Berg 1995). Increases in fine sediment can also cause behavioral and physiological shifts in aquatic insects such as increased drift (Rosenberg and Wiens 1978, Culp et al. 1985), altered respiration (Lemley 1982), and impeded filter feeding (Strand and Merritt 1999). Because stream-dwelling taxa have various preferences for particle size and tolerances to disturbance, sedimentation can result in community-level effects (Lenat et al. 1981, Rader and McArthur 1995, Hubert et al. 1996).

In streams where riffle habitats have been infilled by fine sediment and no longer function as suitable coarse-textured habitat, insects must either 1) rely on other locations within the stream where they can survive and complete their larval development, or 2) abandon the stream reach altogether. In the former case, bank habitats on the margins of streams or snag habitats may serve as refugia for insects that can no longer find stable habitats in fine-textured riffles. Examples of invertebrate refugia include use of snag habitat in high-flow events (Borchardt 1993, Lancaster and Hildrew 1993a, Biggs et al. 1997, Swanson et al. 1998, Rempel et al. 1999) and in streams with naturally unstable sandy bottoms (Dudley and Anderson 1982, Benke et al. 1985, Hawkins and Sedell 1990, Wallace et al. 1996). This concept of the use of refugia in response to landscape-level disturbance complements previous concepts of stable habitat refugia in streams.

The purpose of our study was to determine the effects of land cover type and associated changes in physical and chemical characteristics on the habitat distribution of stream insects. Our objectives were to 1) identify habitat-specific insect assemblage responses to geomorphic and chemical characteristics associated with land cover change, 2) analyze assemblage response to sedimentation based on insect habitat preferences, and 3) discuss implications of these habitat-specific results on sampling protocols used in bioassessment studies. We hypothesized that 1) insects residing in riffles and pools would be most affected by fine sediment disturbance, whereas insects residing on bank vegetation or snags would be most affected by chemical disturbance, 2) a greater proportion of facultative insect taxa (those found in all habitats sampled) would occur in banks vs other

habitats in sediment-disturbed streams because of the greater relative stability of bank substrate, and 3) the distribution of aquatic insects may shift from one habitat (e.g., riffles) to another (e.g., banks) as a result of streambed disturbance.

Study Sites

Twenty-nine sites within the Etowah River catchment (4823 km²) in the Piedmont region of north-central Georgia, USA, were selected for this study (Fig. 1). The region has a temperate climate with a mean annual rainfall of 132 to 163 cm. Selected study streams had relatively low gradients (0.001–0.009), and streambeds were primarily composed of sand and gravel (mean $\phi = -2.9$; $\phi = -\log_2$ diameter in mm; Gordon et al. 1992). The Etowah catchment lies north of Atlanta, Georgia, and recent development has potentially impacted many of the streams. Study sites were divided into 3 catchment size classes (15, 50, and 100 km² \pm 25%) that exhibited a range in urban (5–61%), forest (27–87%), and agricultural (7–38%) land cover. Streams had no point sources of pollution near the selected 100-m sampling reach. These systems are not influenced by snowmelt, so base-flow conditions occur year-round except following large storm events.

Three primary habitat types were defined within stream reaches: riffles, pools, and banks. Riffles were characterized by regions of relatively shallow depth, fast water velocities, coarse-textured sediment, and relatively steep gradients, compared to other parts of the reach. Pools were associated with relatively deep, slow-moving water and relatively low gradients. Banks, the margins of the streams, ranged in vegetative structure, including snags, sticks, rootmats, leaf-packs, grass, and moss.

Methods

Environmental sampling

Percent land cover (urban, agriculture, forest) for the catchments in our study were determined using 1997 *Landsat* TM images (30-m resolution; Lo and Yang 2000). Urban land cover included high-density land (primarily commercial/industrial) and low-density land (primarily residential). Agricultural land cover included

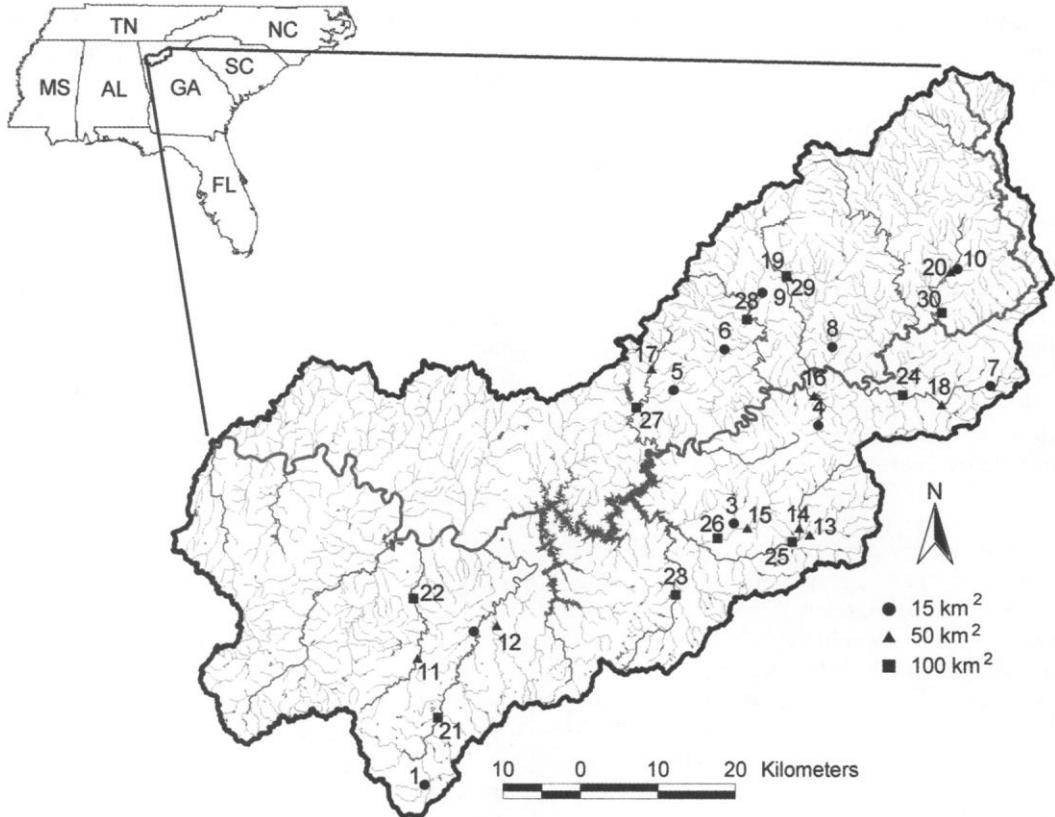


FIG. 1. The 29 study sites within the Etowah River catchment, Georgia, USA. Symbols indicate size class of catchments of the streams studied ($15, 50, \text{ and } 100 \text{ km}^2 \pm 25\%$). Sample reaches were located at the base of each catchment.

cultivated/exposed land and cropland/grassland. Forested land cover included evergreen, deciduous, and mixed forests.

Geomorphic and morphometric variables were measured from May to August 1999. Stream gradient was surveyed with a total station instrument as the slope of the line connecting tops of riffles within the reach ($\sim 100\text{-}, 150\text{-}, \text{ or } 200\text{-m}$ length depending on catchment size). We determined proportion of area within the reach that was riffle, pool, or bank to weight invertebrate variables by habitat area. Riffle and pool areas were estimated by taking measurements along the thalweg of the stream. Bank area was estimated by measuring depth and length of submerged vegetation along both banks for a 100-m reach. Water depth and modal particle size (used to obtain mean particle size for the reach) were measured along 5 transects parallel to banks that were spaced at 10,

30, 50, 70 and 90% of stream width. Each transect had 17 sample points except for the 50% transect, which had 34, for a total of 102 measurements. Bed sediment was collected from distinct geomorphic units (riffles and pools) by compositing three 1-L grab samples obtained from separate locations. These bed sediment samples were oven-dried and sieved to determine particle-size distribution in whole phi intervals. Bed sediment mobility was calculated as the ratio of available tractive force to critical tractive force needed to move the average bed sediment during the 0.5-y recurrence interval flood, which was determined using the US Geological Survey rural flood frequency curves (Stamey and Hess 1993) and adjusted for the % total impervious land cover in the catchment by equation 10.6 of Dunne and Leopold (1978). The critical tractive force was calculated using the average size in mm of the bed sediment by

equation 7.18 of Gordon et al. (1992). High values for bed mobility correspond to high potential for displacement of bed sediment. Wetted large woody debris was measured as all wood that was in contact with the water during base-flow conditions. The length and diameter of each piece >10 cm in diameter was recorded to derive the total volume per stream reach.

Mean annual water chemistry values (measured monthly from April 1999 to 2000 during baseflow) were used in analyses. Specific conductance, pH, and dissolved oxygen (DO) were collected with a Hydrolab® Datasonde 4. Turbidity was measured with a Hach® turbidimeter. Water samples were field-filtered (GFF, 0.45- μ m pore size) and brought back to the laboratory for nutrient analyses ($\text{NH}_4\text{-N}$, $\text{NO}_3/\text{NO}_2\text{-N}$, and soluble reactive P [SRP]) using standard methods (APHA 1989). An additional water sample was taken and filtered on pre-ashed and weighed filters to obtain total suspended solids (TSS).

Macroinvertebrate sampling

Benthic macroinvertebrates were sampled at the sites from March to April 1999 during base-flow conditions. Three replicate, quantitative samples were randomly taken in unique riffle, pool, and bank habitats. Replicates were taken at different locations within a single habitat unit where there were <3 distinct replicate habitat units within a 100-m reach.

Riffle samples were taken using a Surber sampler (0.09 m², 500- μ m mesh) to a depth of 10 cm for 3 min. For pools, a stove-pipe corer (0.04 m²) was placed into the substrate, and all sediment \leq 10 cm deep was removed and washed through a 500- μ m sieve. Bank habitats were sampled at random locations along the stream length with vertical relief (i.e., not lateral gravel bars). A rectangular dip net (500- μ m mesh) was swept along a 1-m section of stream bank 3 times just below the water surface (0.2-m depth) along the channel margin while vigorously agitating the substrate. Thus, the sample had a 0.2-m² area. All samples were elutriated in the field and poured through a 500- μ m sieve. Organic debris and invertebrates were preserved in 10% formalin and returned to the laboratory for sorting.

All large invertebrates (>1 mm length) were hand-picked from debris using a dissecting mi-

croscope at 15 \times and preserved in 70% ethanol. Smaller invertebrates (0.5–1.0 mm length) were subsampled using a wheel sample splitter (Waters 1969) if there were >100 organisms. The invertebrates were later counted, and identified to the lowest taxonomic unit feasible, typically genus, using standard keys (Brigham et al. 1982, Merritt and Cummins 1996, Wiggins 1996). Chironomids were identified as Tanytopodinae or non-Tanytopodinae. Non-insects were identified to order. Only insect taxa, which composed 86% of total taxa richness among sites (115 taxa), were used for analyses (except for biotic index calculations) to obtain taxonomic consistency when assigning habitat preferences and analyzing responses to disturbance. Other abundant macroinvertebrates included Oligochaeta and *Corbicula* spp.

Data analyses

Insect taxa richness (no. of taxa) and density (no./m²) were calculated for each habitat. All densities were $\log_{10}(x)$ transformed prior to analyses. Total insect density and density excluding chironomids were compared among riffle, pool, and bank habitats using a 1-way ANOVA. Two biotic indices, the Family Biotic Index (FBI; Hilsenhoff 1988) and the North Carolina Biotic Index (NCBI; Lenat 1993) and 2 multi-metric indices, the Benthic Index of Biotic Integrity (B-IBI; Kerans and Karr 1994) and the Invertebrate Community Index (ICI; Ohio EPA 1989), were calculated for invertebrates in all habitats using habitat-weighted densities, and also exclusively for riffle habitats to compare results using typical sampling approaches (i.e., biomonitoring based on riffle sampling vs composite multihabitat sampling). Differences in invertebrate scores between habitats (all habitats vs riffle habitats) were compared using *t*-tests (2-sample, assuming equal variances).

Insect richness and density in the 3 different habitats were used as dependent variables in correlations with physical habitat and water-quality variables. Only single variables from any autocorrelated groups ($r > 0.80$) were selected for use in analyses. Selection from autocorrelated groups was biased towards variables that are typically collected as part of other sampling protocols. All environmental variables were checked for normality and appropriately transformed, if necessary. Two variables were select-

ed to represent sediment conditions on the streambed: mean bed sediment size (ϕ) and bed mobility. These variables were chosen out of the >50 geomorphic and sediment variables measured because they are good representations of both static and dynamic sedimentology of the streambed and they reflect the fundamental attributes of fine sediment that can be detrimental to insects. Regression analyses were used to identify relationships between insect assemblages and these sediment variables. In addition, % bank richness (bank richness/bank + riffle richness) was regressed against mean ϕ and bed mobility to test if there was a greater proportion of taxa richness in banks vs riffles with increased fine sediment. Relationships were also determined between sediment disturbance and groups of insect taxa defined as *obligate* or *facultative* among habitats. Obligate taxa were found exclusively in a habitat at every site. Facultative taxa were found at multiple habitats. Rare taxa (i.e., only found at 1 site for each habitat) were excluded.

Sites were divided into 2 groups (sediment-impacted and minimally impacted) based on levels of sediment disturbance to determine whether there were differences in representation by facultative taxa between groups of streams that differed in sediment characteristics. Sites were ordered within size classes (15, 50, and 100 km² \pm 25%) according to mean ϕ and bed mobility. The 3 sites with the largest particle sizes and lowest bed mobility (minimally impacted) and 3 sites with the smallest particle sizes and highest mobility (sediment-impacted) were selected within each of the 3 catchment size classes, resulting in 2 groups of 9 sites. Insect assemblage measures were then compared between these 2 groups of sites using *t*-tests.

Results

Physical and biological differences among habitats

Sites exhibited a relatively large range in values of variables related to sedimentation (Table 1). Mean ϕ ranged from -0.3 (very coarse sand) to -6.4 (small cobble) across sites, with a mean of -2.8 (fine gravel). Bed mobility ranged from 0.5 to 27.3. Twenty-three sites had bed mobility ratios >1 , indicating that the stream had energy to move the mean particle size more of-

ten than the 0.5-y recurrence interval flood for these sites (Table 1).

Mean richness differences could not be compared across habitats because different areas were sampled (pool = 0.12 m², riffle = 0.27 m², bank = 0.60 m²). Bank richness was highest overall (Table 2), but was lower when standardized for area (an intermediate value of 0.20 m² was used; pool = 14.4, riffle = 14.8, bank = 9.6). Average total insect density was not significantly different across habitats, but density of non-chironomid taxa was highest in riffles (Table 2).

Habitat-specific responses to disturbance

Many of the geomorphic and chemical variables that were correlated with % urban and forested land cover (Roy et al. 2003) were correlated with riffle insect richness and density and pool insect density (Table 3). Taxa richness in riffle habitats was positively related to increased slope, depth, % riffle area, bed sediment variability, and DO, and negatively related to fine bed sediment size (mean, riffle, and pool ϕ), bed mobility, NH₄-N, SRP, specific conductance, and TSS. Riffle density was correlated with fewer environmental variables compared to richness measurements (10 and 14, respectively). Pool richness was negatively related to SRP, whereas pool density was correlated with numerous physical habitat (7) and water quality variables (3).

Bank richness was positively correlated with bed sediment variability and negatively correlated with specific conductance. Bank density was positively related to bed sediment variability and negatively related to riffle bed sediment mobility (Table 3).

Macroinvertebrates

Our analyses included 91 aquatic insect taxa from the 115 collected (24 were considered rare and excluded). Fifteen insect taxa were considered obligate riffle dwellers, 31 taxa were obligate bank dwellers, and 45 taxa were considered facultative and occurred in all habitats (Appendix). No taxa were exclusive to pool habitats, so for simplicity in comparing riffle and bank habitats, pool habitats were ignored. Thus, *Psephenus* spp. (Coleoptera) and Tanyderidae (Diptera), which were found only in riffle and pool habitats, were included with obligate riffle taxa, and

TABLE 1. Land cover, morphometric, geomorphic, and biotic characteristics of the 29 sites within the Etowah River catchment. Insect richness and density values are totals of 3 replicate samples for each habitat.

No.	Site Name	1997 land cover (%)			Bank full width (m)	Bank full depth (m)	Mean phi	Bed mobility	Richness			Density (no./m ²)				
		Forest	Urban	Agri-culture					Slope	Riffle	Pool	Bank	Riffle	Pool	Bank	
1	Pumpkinvine Creek	16.6	76.2	10.5	12.7	0.003	11.4	1.5	-1.7	3.9	21	6	21	1326	950	472
3	Avery Creek ^a	22.3	40.3	19.8	38.4	0.002	6.7	0.5	-1.1	8.6	7	2	25	1104	533	1598
4	Smithwick Creek ^a	15.6	49.3	13.3	37.0	0.003	9.7	0.9	-2.0	3.2	21	4	27	2644	267	615
5	McCanless Creek	13.1	67.0	9.4	23.1	0.003	8.7	1.2	-3.6	0.9	21	17	33	2322	2242	2377
6	Bluff Creek ^b	14.5	67.1	7.7	24.4	0.004	8.1	1.6	-5.0	0.6	24	10	24	1674	1175	840
7	Settingdown Creek ^a	17.1	55.0	16.1	27.5	0.002	11.7	2.0	-0.3	9.0	7	4	34	489	283	1015
8	Conn's Creek	14.9	87.0	6.4	6.5	0.006	8.4	1.2	-4.9	1.0	24	11	36	1215	2483	2298
9	Polecat Branch ^b	11.3	43.2	16.0	37.7	0.009	6.8	1.1	-6.4	0.5	18	11	21	2963	2875	1557
10	Burr Creek ^b	12.2	56.1	15.9	26.8	0.008	10.7	1.2	-6.1	0.6	23	11	13	1644	1333	377
11	Raccoon Creek	50.7	68.3	10.6	21.0	0.003	16.8	1.6	-3.4	1.7	22	6	31	1696	2450	1303
12	Little Pumpkinvine Creek ^b	52.0	63.4	24.2	11.8	0.005	23.5	2.4	-3.2	2.9	19	2	38	1633	242	2053
13	Chicken Creek ^a	59.1	47.1	29.9	22.0	0.002	11.8	2.0	-0.8	7.5	13	3	26	1752	583	717
14	Little River ^a	44.1	58.0	14.6	26.2	0.003	13.2	1.7	-1.4	7.7	21	4	22	2759	292	1850
15	Mill Creeks ^a	50.7	48.8	15.4	34.8	0.002	18.7	2.9	-1.5	4.1	16	4	28	415	275	1227
16	Smithwick Creek	38.6	59.6	11.0	29.1	0.005	15.6	1.9	-3.8	2.1	27	10	31	1904	1817	2448
17	Shoal Creek, Cherokee Co.	53.2	77.2	7.0	15.2	0.003	13.0	1.5	-3.4	1.4	13	7	35	604	592	873
18	Settingdown Creek	53.6	47.7	18.7	32.5	0.002	13.9	2.0	-1.1	6.2	19	6	39	2004	1433	1900
19	Darnell Creek ^b	60.3	85.1	4.9	8.4	0.004	12.2	1.8	-3.9	1.9	19	5	31	1096	558	872
20	Shoal Creek, Dawson Co. ^b	53.8	70.8	11.2	17.5	0.007	16.3	2.0	-5.1	1.5	34	7	36	3222	2683	2272
21	Pumpkinvine Creek ^a	125.7	77.3	10.8	11.0	0.001	20.6	2.7	-0.5	6.0	11	3	24	637	108	568
22	Raccoon Creek	108.5	73.7	8.1	17.7	0.003	25.2	1.5	-3.1	1.7	31	15	32	1522	2825	1343
23	Noonday Creek ^a	85.4	27.2	60.7	11.2	0.002	18.8	2.4	-1.2	6.2	5	2	13	115	100	232
24	Settingdown Creek ^b	96.1	48.6	18.4	31.8	0.002	17.6	2.1	-2.1	4.0	33	13	40	3748	2792	2807
25	Little River	122.1	52.0	22.6	24.3	0.001	15.7	2.2	-0.7	7.4	9	34	25	341	1250	1253
26	Mill Creeks ^a	84.6	45.5	18.8	34.6	0.001	21.0	1.5	-0.7	5.9	7	2	29	304	392	1283
27	Shoal Creek, Cherokee Co.	102.0	75.3	8.5	15.8	0.003	25.5	3.1	-3.0	2.3	26	11	34	1696	808	1267
28	Sharp Mountain Creek	103.9	61.0	10.0	26.9	0.007	24.1	2.2	-5.5	0.9	21	5	27	2393	2717	878
29	Long Swamp Creek ^b	77.4	85.0	5.0	8.6	0.004	20.0	2.0	-4.6	1.0	17	8	26	841	958	653
30	Shoal Creek, Dawson Co. ^b	90.7	76.1	10.1	13.5	0.003	22.0	2.7	-3.7	3.0	36	34	32	4374	5733	870
Mean		56.9	61.7	15.0	22.3	0.004	15.4	1.8	-2.9	3.6	19.5	8.9	28.7	1670.2	1405.2	1304.1
SE		6.7	2.8	2.0	1.8	0.0004	1.1	0.1	-0.3	0.5	1.5	1.5	1.3	198.2	237.5	129.2

^a Sediment-impacted sites as determined in Methods

^b Minimally impacted sites as determined in Methods

TABLE 2. Riffle, pool, and bank richness and density values (mean \pm 1 SE). Results are shown from 1-way ANOVA for comparison of mean densities among riffle, pool, and bank habitats. Richness values could not be statistically compared because of different areas sampled.

	Richness (no. taxa)	Density (no./m ²)	
		Total	Excluding chironomids
Riffle	19.5 (1.5)	1670.2 (198.2)	957.1 (130.3)
Pool	8.9 (1.5)	1405.2 (237.5)	312.6 (82.4)
Bank	28.7 (1.3)	1304.1 (129.2)	481.2 (69.1)
F		0.955	11.3
p		0.389	<0.001

Progomphus spp. (Odonata), which was found exclusively in bank and pool habitats, was included with obligate bank taxa.

Sedimentation effects on insect distribution

Fine bed sediment and high bed mobility were significantly related to low richness and density (all habitats), and low riffle insect richness and density, but there was no relationship with bank richness or density (Table 4). Proportional bank richness increased with decreased particle size (Fig. 2A) and increased bed mobility (Fig. 2B), explaining 43 and 35% of the variation in % bank richness, respectively.

Examination of relationships with sediment variables based on insect habitat preferences in riffles indicated that both obligate and facultative taxa richness and density significantly decreased with fine bed sediment and high bed mobility (Table 5). In banks, neither obligate nor facultative taxa richness or density were correlated with mean phi or bed mobility (Table 5).

Comparison of minimally impacted vs sediment-impacted sites

Categorizing sites as sediment-impacted vs minimally impacted resulted in 2 significantly different groups of sites based on both mean phi and mean bed mobility. The scores for mean phi were significantly different between the 9 minimally impacted (-4.44) and 9 sediment-impacted (-1.05) sites ($t = 6.87$, $p < 0.001$) shown in Table 1. Mean bed mobility was also significantly different between minimally impacted

(1.77) and sediment-impacted (6.47) sites ($t = 6.09$, $p < 0.001$).

Richness of facultative taxa in riffles was lower in sediment-impacted sites compared to minimally impacted sites (11.0 vs 20.2); however, richness of facultative taxa in banks was similar between disturbance groups (20.1 vs 22.7; Fig. 3A). Density of facultative taxa was also significantly different between minimally impacted and sediment-impacted sites in riffles (2249/m² vs 1115/m²), but taxa had similar densities in banks (1352/m² vs 997/m²; Fig. 3B).

Biotic indices in riffles vs all habitats

There was no consistent response when biotic indices from riffles vs all habitats were compared (Table 6). Water quality was higher in riffles than in all habitats for FBI and NCBI, but ICI indicated the opposite. B-IBI scores were similar for riffles and all habitats.

FBI and NCBI differed for sediment-impacted and minimally impacted sites from riffles (FBI: 4.03 vs 3.47, $t = 2.25$, $p = 0.019$; NCBI: 4.19 vs 3.49, $t = 2.75$, $p = 0.007$), but not from all habitats (FBI: 5.47 vs 5.18, $t = 1.12$, $p = 0.139$; NCBI: 5.70 vs 5.29, $t = 1.65$, $p = 0.060$). Higher scores for FBI and NCBI in sediment-impacted riffles reflected lower water quality compared to minimally impacted riffles.

Discussion

Habitat-specific responses to reach-scale physical and chemical disturbance

Our analyses suggest that insects in riffles, rather than pool and bank habitats, were most sensitive to physical and chemical changes resulting from land cover change, so riffles are important to sample to detect these changes. Density and richness of assemblages in riffle habitats were highly correlated with many environmental variables measured, whereas these relationships with invertebrate assemblages in pool and bank habitats were weaker or nonexistent. Biotic indices of water quality differed in riffle habitats between streams we characterized as minimally or sediment-impacted, but did not differ when all habitats were considered. Riffles are critical habitats in stream ecosystems, in which they can harbor unique assemblages not found in finer-textured bed sediment (Plafkin et

TABLE 3. Summary information for physical habitat and water-quality variables, along with Pearson's correlation coefficients (r) between environmental variables and insect richness and density (no./m²) in riffle, pool, and bank habitats ($n = 29$ sites). Sign (+/-) indicates direction of relationship. ^{u,a,f} indicates a significant regression ($p < 0.05$) between the environmental variable and total 1997 % urban (u), agriculture (a), and/or forested (f) land cover, respectively (for r^2 values, see Roy et al. 2003). Forested land cover is negatively correlated with both urban land cover ($r = 0.81$) and agriculture land cover ($r = 0.72$). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Mean	SD	Riffle			Pool			Bank		
			Richness	Density	Richness	Density	Richness	Density	Richness	Density	
Physical habitat											
^w Slope (energy grade line) ^a	-2.54	0.26	+0.56**	+0.55**	+0.04	+0.56**	+0.05	+0.17			
Depth (cm) ^a	+1.40	0.13	+0.37*	+0.33	+0.26	+0.24	+0.34	+0.03			
Bed sediment size variability	+2.11	0.68	+0.66***	+0.63***	+0.24	+0.53**	+0.41*	+0.47**			
^w Mean bed sediment size (phi)	-2.88	1.81	-0.55**	-0.48**	-0.18	-0.61***	+0.02	-0.09			
^w Riffle bed sediment size (phi)	-2.83	1.44	-0.76***	-0.65***	-0.35	-0.67***	-0.28	-0.27			
^w Pool bed sediment size (phi)	-1.37	1.19	-0.42*	-0.30	-0.10	-0.34	+0.10	+0.08			
^w Bed sediment size mobility ^a	+0.41	0.39	-0.46*	-0.38*	-0.15	-0.56**	+0.03	-0.05			
^w Riffle bed sediment size mobility ^a	-0.16	0.33	-0.63***	-0.53**	-0.20	-0.42*	-0.23	-0.39*			
^w Riffle area (%) ^b	+0.47	0.25	+0.51**	+0.38*	+0.24	+0.63***	+0.08	+0.24			
Wetted large woody debris (m ³ /m ²) ^c	-2.65	0.24	+0.13	-0.09	-0.06	-0.22	+0.14	-0.04			
Water quality											
^w Total suspended solids (mg/L) ^a	+0.61	0.29	-0.52**	-0.30	-0.06	-0.32	+0.07	+0.10			
^{u,a,f} NH ₄ -N (µg/L) ^a	+1.32	0.29	-0.51**	-0.28	-0.12	-0.27	-0.24	-0.04			
^{u,a,f} NO ₃ /NO ₂ -N (µg/L)	+368	239	-0.21	-0.08	-0.18	-0.07	-0.14	-0.02			
^w Soluble reactive P (µg/L)	+77.3	34.8	-0.59**	-0.42*	-0.38*	-0.57**	-0.14	+0.04			
^w Specific conductance (µs/cm)	+69.1	30.9	-0.66***	-0.56**	-0.34	-0.53**	-0.37*	-0.23			
^{a,f} Turbidity (NTU) ^a	+0.84	0.19	-0.34	+0.03	-0.08	-0.21	-0.01	+0.03			
pH	+7.09	0.23	-0.17	-0.18	-0.22	-0.21	-0.05	-0.14			
^w Dissolved oxygen (mg/L)	+8.60	0.44	+0.62***	+0.37*	+0.18	+0.37*	+0.20	+0.06			

^a Log₁₀(x) transformed
^b Arcsin square-root transformed
^c Log₁₀(arcsin square-root) transformed

TABLE 4. Linear regression models (r^2 values) between insect richness and density (no./m²) and mean phi (bed sediment size) and bed mobility for 29 sites. All habitats = riffle + pool + bank habitats. (–) indicates original negative direction of relationship. * = $p < 0.05$, ** = $p = 0.01$.

	Mean phi (–log ₂ mm)	Bed mobility
All habitats		
Richness	(–) 0.14*	0.10
Density	(–) 0.24**	(–) 0.22*
Riffle habitats		
Richness	(–) 0.26**	(–) 0.21*
Density	0.12	(–) 0.14*
Bank habitats		
Richness	0.00	0.00
Density	0.01	0.00

al. 1989). Further, riffles can be habitats with the highest invertebrate biomass (Rosenfeld and Hudson 1997, Ramirez et al. 1998) and density (Ramirez et al. 1998).

Bed sediment variables and specific conductance were the most important predictive variables for invertebrates in all 3 habitats. These results are consistent with our findings for all habitats combined (Roy et al. 2003). We originally hypothesized that insects in riffle and pool habitats would be more sensitive to sediment than chemical disturbance, whereas insects in banks would be more sensitive to chemical than physical disturbance. However, we found that correlations could be as high for sediment and chemical variables in riffle and pool assemblages, and these same relationships were significant, yet weaker, in bank assemblages. In addition, specific conductance, the chemical variable most highly correlated with overall richness, was more highly correlated with riffle assemblages than bank assemblages, refuting our hypothesis that chemical variables were most important to bank assemblages. Sediment-related variables were slightly more important than chemically related variables in producing differences between riffle and bank assemblages. Models were weaker between chemical variables and % bank richness (e.g., best fit: SRP vs % bank richness, $r^2 = 0.30$) than the models using mean sediment size and bed mobility ($r^2 = 0.43$ and 0.35 , respectively). Thus, invertebrates in all 3 habitats were related to chemistry and

sediment, but sediment was more important in determining interhabitat variation.

Banks as refugia in sediment-disturbed streams

The positive relationship between % bank richness and sedimentation suggests that insects reside primarily in bank habitats at sites where riffle quality is poor. Negative effects of fine sediment were greater for riffle-dwelling than bank-dwelling obligate and facultative taxa. Facultative taxa occurred in riffles and banks in similar proportions when streams had large and stable bed sediments. However, facultative taxa may prefer bank habitats (i.e., snags or rooted aquatic vegetation) when there are high levels of fine sediment, as shown by the greater difference in bank vs riffle richness at sediment-impacted than minimally impacted sites. Streams with large amounts of fine sediment in the riffles may be functioning similarly to low-gradient, sandy bottomed streams, where most invertebrate production is in marginal snag habitats (e.g., Benke et al. 1985, Rader and McArthur 1995, Wallace et al. 1996). These shifts in the microdistribution of the benthos are consistent with our hypothesis that banks serve as refugia in streams where riffle habitat quality is poor.

Refugia have been defined as places not subject to hydraulic stress (Lancaster and Hildrew 1993b) or, more generally, as areas not impacted by disturbance, where density independent losses are small (Hawkins and Sedell 1990, Sedell et al. 1990). Types of refugia include large stable bed particles with interstitial spaces (Townsend 1989, Borchardt 1993), dead zones with low shear stress (Lancaster and Hildrew 1993b), and the hyporheic zone (Palmer et al. 1992). Woody debris often serves as refugia during floods (Dudley and Anderson 1982, Borchardt 1993, Lancaster and Hildrew 1993a, Rader and McArthur 1995). Our data showed that bank habitats may also become refugia for insects that typically reside in riffle habitats in streams disturbed by fine sediment. The greater proportion of facultative taxa in bank habitats in sediment-impacted than minimally impacted sites (not just obligate bank taxa), supports this idea.

Implications for biomonitoring

Known effects of disturbance on the spatial distributions of biota should be incorporated

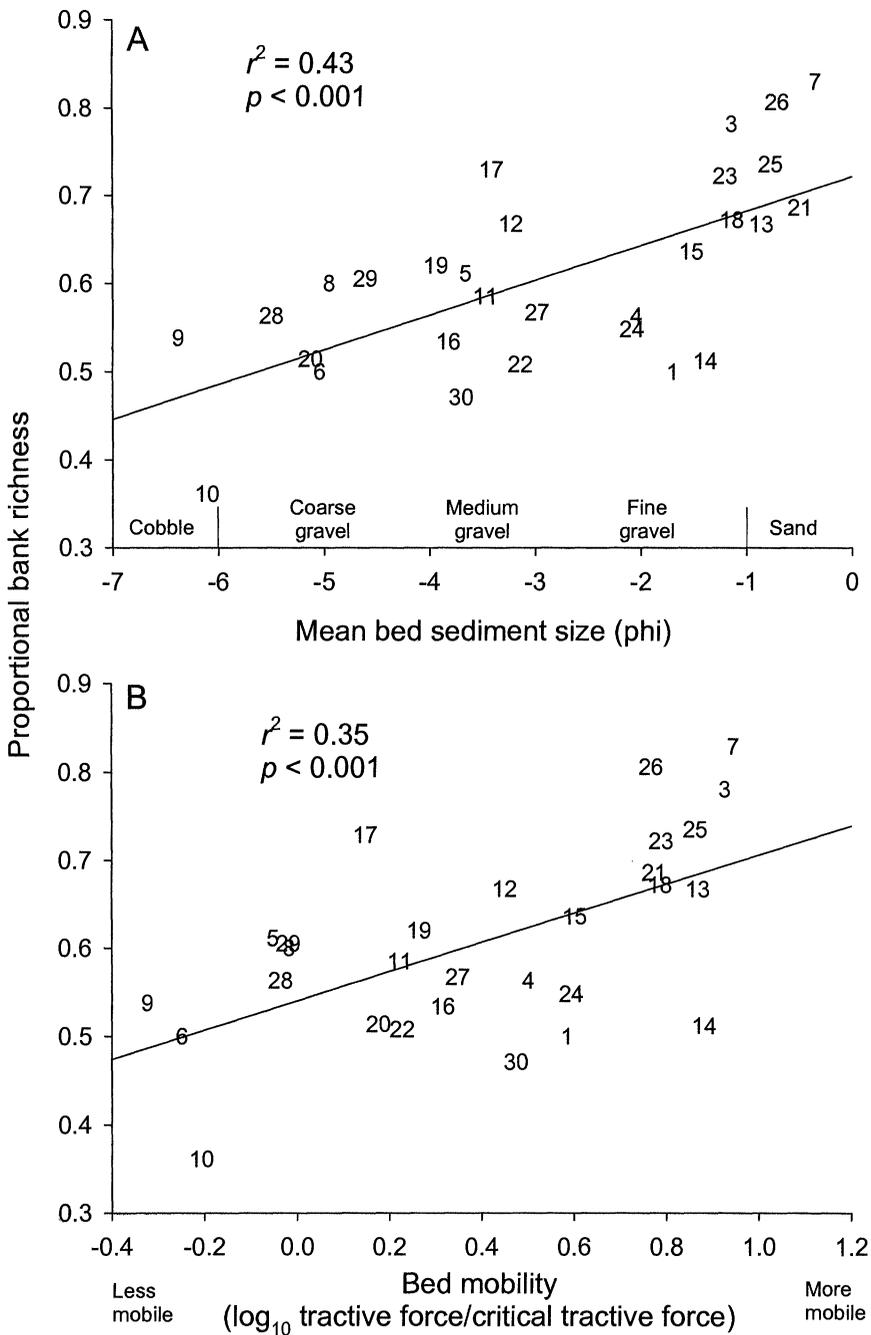


FIG. 2. Linear regression for proportional bank richness (bank richness/riffle + bank richness) with mean bed sediment size (A) and bed mobility (B). Numbers are sites (Table 1).

into sampling regimes for stream bioassessment. Our study showed relatively greater effects of disturbance on taxa inhabiting riffles vs pools and banks. Thus, if biomonitoring studies

sample >1 habitat, conclusions drawn may vary according to the habitat sampled (Kerans et al. 1992). By sampling quantitatively in riffle, pool, and bank habitats, we were able to detect dis-

TABLE 5. Linear regression models (r^2 values) for obligate and facultative taxa richness and density (no./m²) found in riffle and bank habitats (for 29 sites) vs sedimentation variables. (-) indicates original negative direction of relationship. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Mean phi ($-\log_2$ mm)	Bed mobility
Riffle habitats		
Obligate taxa		
Richness	(-) 0.34***	(-) 0.21*
Density	(-) 0.46***	(-) 0.37***
Facultative taxa		
Richness	(-) 0.23**	(-) 0.17*
Density	(-) 0.46***	(-) 0.33**
Bank habitats		
Obligate taxa		
Richness	0.01	0.01
Density	0.00	0.00
Facultative taxa		
Richness	0.00	0.00
Density	0.00	0.00

turbances occurring within single habitats, and relative changes in assemblages across habitats. However, replicate, quantitative sampling is time consuming and expensive. Laboratory sorting (excluding identification) took 1.5 h/sample for riffle habitats, 1.6 h/sample for pool habitats, and 4.2 h/sample for bank habitats. The US Environmental Protection Agency's Rapid Bioassessment Protocol (RBP) for invertebrates (Barbour et al. 1997) typically involves field picking and sorting of invertebrates for a set time, which is less costly than quantitative sampling. However, the RBP procedure of combining samples from all habitats may miss changes occurring within single habitats, which might be averaged across habitats in qualitative sampling.

Our data suggest that sampling exclusively in riffle habitats may be adequate for bioassessment, at least in sediment-impaired streams, where riffle habitats are more susceptible to sediment disturbance than other habitats. Previous work has also suggested that stream assessment using a riffle sampling can discern human influence on streams and is cost-effective (Plafkin et al. 1989, Kerans and Karr 1994, Karr and Chu 1997). Because numerous variables other than physical habitat influence the distri-

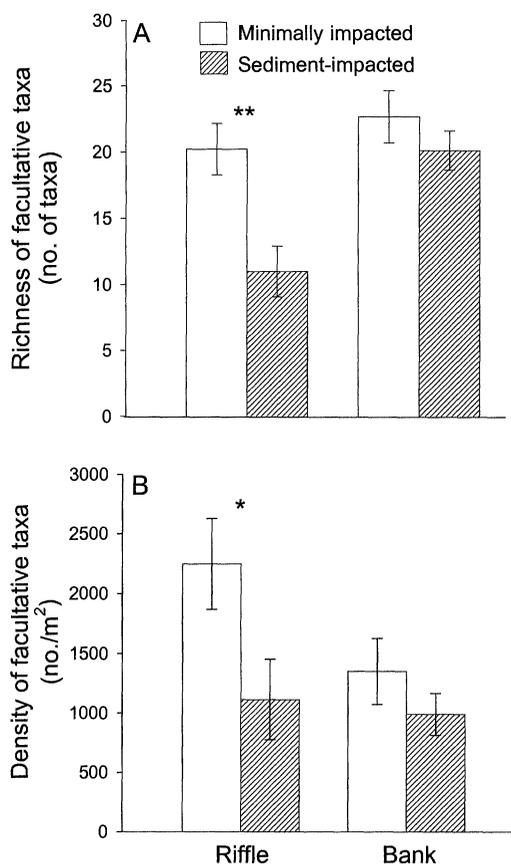


FIG. 3. Comparison of facultative taxa (found in all habitats sampled) richness (A) and density (B) between minimally impacted and sediment-impacted sites in riffles and banks (2-sample t -tests, $n = 18$ for each test, * = $p < 0.05$, ** = $p < 0.001$).

bution of insects (e.g., insect tolerances, season sampled, etc.), dealing with a single habitat may also be a way to control natural variation to detect disturbance in streams. Parsons and Norris (1996) claimed that bioassessment studies that sample only one habitat eliminate the risk of 1) interhabitat variation being mistaken for biological impairment, or 2) habitat-specific biotic variation masking disturbance effects. Consistent with Parsons and Norris (1996) and Hewlett (2000), our results showed that sampling in a single habitat was most effective at detecting disturbance.

Riffle habitats were most sensitive to sediment disturbance, but bank habitats harbored most invertebrate diversity (up to 76% of the total invertebrate richness in the sampled streams). Therefore, sampling banks may be

TABLE 6. Mean (and range) of macroinvertebrate index scores based on taxa collected from riffle habitats and taxa collected from all habitats (riffle + pool + bank). Results from 2-sample *t*-test (assuming equal variances; $n = 29$ for each test) comparing scores for riffles vs all habitats are shown. FBI = Family Biotic Index, NCBI = North Carolina Biotic Index, B-IBI = Benthic Index of Biotic Integrity, ICI = Invertebrate Community Index. Low values for FBI and NCBI scores = high water quality; high values of B-IBI and ICI scores = high water quality.

	Riffles	All habitats	<i>t</i>	<i>p</i>
FBI	3.62 (2.06–4.94)	5.22 (3.89–5.97)	9.44	<0.001
NCBI	3.74 (2.08–5.07)	5.38 (4.24–6.18)	9.61	<0.001
B-IBI	66.5 (37.2–93.4)	69.3 (44.0–91.9)	0.83	0.204
ICI	51.3 (10.6–85.8)	60.4 (24.7–85.9)	1.86	0.034

critical in studies aimed at understanding invertebrate diversity or distributional shifts in taxa. In addition, richness increased in bank habitats as a function of disturbance, which suggest the importance of sampling banks in streams with significant anthropogenic influence, if taxa richness and diversity are of interest.

The different results obtained by the invertebrate biotic indices (FBI and NCBI) and metric indices (B-IBI and ICI) using riffles vs all habitats may reflect as much about how these metrics are calculated as about the different habitats sampled. The biotic indices are based on invertebrate tolerance scores (Hilsenhoff 1988, Lenat 1993), whereas the metric indices are largely based on diversity (Ohio EPA 1989, Kerans and Karr 1994). Thus, the biotic indices showed that riffles had higher water quality than all habitats combined, whereas the metric indices showed the influence of sampling a variety of habitats in yielding similar or higher water-quality results than for riffles alone.

In conclusion, it is widely known from work in conservation biology that species most vulnerable to extirpation are those with narrow rather than broad habitat requirements (Meffe and Carroll 1977). Over 50% of the 91 insect taxa sampled from all habitats were found only in one habitat (i.e., were obligate taxa). In fact, many obligate riffle-dwelling taxa did

not occur in some of the most disturbed streams, whereas facultative taxa fared much better. Although banks can serve as refugia for invertebrate diversity over short terms while riffle quality is poor, narrow preference ranges of certain taxa will affect their distribution within a stream over longer time scales (Cummins and Lauff 1968). Thus, long-term maintenance of diverse biotic assemblages requires many different habitats, including high-quality riffles and banks.

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Literature Cited

- APHA (American Public Health Association, American Water Works Association, and Water Pollution Control Federation). 1989. Standard methods for the examination of water and wastewater. 17th edition. American Public Health Association, Washington, DC.
- BARBOUR, M. T., J. GERRITSEN, B. D. SNYDER, AND J. B. STRIBLING. 1997. Revision to rapid bioassessment protocols for use in streams and rivers: periphyton, benthic macroinvertebrates, and fish. EPA 841-0-97-002. Office of Water Regulations and

- Standards, US Environmental Protection Agency, Washington, DC.
- BENKE, A. C., R. L. HENRY, D. M. GILLESPIE, AND R. J. HUNTER. 1985. Importance of snag habitat for animal production in southeastern streams. *Fisheries* 10(5):8-13.
- BIGGS, B. J. F., M. J. DUNCAN, S. N. FRANCOEUR, AND W. D. MEYER. 1997. Physical characterization of microform bed cluster refugia in 12 headwater streams, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31:413-422.
- BORCHARDT, D. 1993. Effects of flow and refugia on drift and loss of benthic macroinvertebrates: implications for habitat restoration in lowland streams. *Freshwater Biology* 29:221-227.
- BRIGHAM, A., W. BRIGHAM, AND A. GNILKA. (EDITORS). 1982. Aquatic insects and oligochaetes of North and South Carolina. Midwest Aquatic Enterprises, Mahomet, Illinois.
- CULP, J. M., F. J. WRONA, AND R. W. DAVIES. 1985. Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* 64:1345-1351.
- CUMMINS, K. W., AND G. H. LAUFF. 1968. The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia* 34:145-181.
- DUDLEY, T., AND N. H. ANDERSON. 1982. A survey of invertebrates associated with wood debris in aquatic habitats. *Melandria* 39:1-21.
- DUNNE, T., AND L. B. LEOPOLD. 1978. *Water in environmental planning*. W. H. Freeman and Company, San Francisco, California.
- GORDON, M. D., T. A. MCMAHON, AND B. L. FINLAYSON. 1992. *Stream hydrology: an introduction for ecologists*. John Wiley and Sons, New York.
- HARDING, J. S., E. F. BENFIELD, P. V. BOLSTAD, G. S. HELFMAN, AND E. B. JONES. 1998. Stream biodiversity: the ghost of land use past. *Proceedings of the National Academy of Sciences of the United States of America* 95:14843-14847.
- HAWKINS, C. P., AND J. R. SEDELL. 1990. The role of refugia in the recolonization of streams devastated by the 1980 eruption of Mount St. Helens. *Northwest Science* 64:271-274.
- HERLIHY, A. T., J. L. STODDARD, AND C. B. JOHNSON. 1998. The relationship between stream chemistry and watershed land cover data in the mid-Atlantic region, USA. *Water, Air, and Soil Pollution* 105:377-386.
- HEWLETT, R. 2000. Implications of taxonomic resolution and sample habitat for stream classification at a broad geographic scale. *Journal of the North American Benthological Society* 19:352-361.
- HILSENHOFF, W. L. 1988. Rapid field assessment of organic pollution with a family-level biotic index. *Journal of the North American Benthological Society* 7:65-68.
- HUBERT, W. A., W. J. LAVOIE, AND L. D. DEBRAY. 1996. Densities and substrate associations of macroinvertebrates in riffles of a small, high plains stream. *Journal of Freshwater Ecology* 11:21-26.
- JONES, R. C., AND C. C. CLARK. 1987. Impact of watershed urbanization on stream insect communities. *Water Resources Bulletin* 23:1047-1055.
- KARR, J. R., AND E. W. CHU. 1997. *Biological monitoring and assessment: using multimetric indexes effectively*. EPA 235-R97-001. University of Washington, Seattle, Washington.
- KERANS, B. L., AND J. R. KARR. 1994. A benthic index of biotic integrity (B-IBI) for rivers of the Tennessee Valley. *Ecological Applications* 4:768-785.
- KERANS, B. L., J. R. KARR, AND S. A. AHLSTEDT. 1992. Aquatic invertebrate assemblages: spatial and temporal differences among sampling protocols. *Journal of the North American Benthological Society* 11:377-390.
- KLEIN, R. D. 1979. Urbanization and stream quality impairment. *Water Resources Bulletin* 15:119-126.
- LAMBERTI, G. A., AND M. B. BERG. 1995. Invertebrates and other benthic features as indicators of environmental change in Juday Creek, Indiana. *Natural Areas Journal* 15:249-258.
- LANCASTER, J., AND A. G. HILDREW. 1993a. Characterizing in-stream flow refugia. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1663-1675.
- LANCASTER, J., AND A. G. HILDREW. 1993b. Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society* 12:385-393.
- LEMLEY, A. D. 1982. Modification of the benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia* 87:229-245.
- LENAT, D. R. 1993. A biotic index for the southeastern United States: derivation and list of tolerance values, with criteria for assigning water-quality ratings. *Journal of the North American Benthological Society* 12:279-290.
- LENAT, D. R., D. L. PENROSE, AND K. W. EAGLESTON. 1981. Variable effects of sediment addition on stream benthos. *Hydrobiologia* 79:187-194.
- LO, C. P., AND X. YANG. 2000. Mapping the dynamics of land use and land cover change in the Atlanta Metropolitan Area using time sequential Landsat images. *ASPRS 2000 Proceedings* (in CD form). Annual meeting held in Washington, DC, 22-26 May 2000. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.
- MEADE, R. H., T. R. YUZYK, AND T. J. DAY. 1990. Movement and storage of sediment in rivers of the United States and Canada. Pages 255-280 *in* M. G. Wolman and H. C. Riggs (editors). *Surface water hydrology. The geology of North America Volume 0-1*. Geological Society of America, Boulder, Colorado.
- MEFFE, G. K., AND C. R. CARROLL. 1997. *Principles of*

- conservation biology. 2nd edition. Sinauer Associates, Inc., Sunderland, Massachusetts.
- 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.
- OHIO EPA (Ohio Environmental Protection Agency). 1989. Biological criteria for the protection of aquatic life, Volumes I-III. Surface Water Section, Division of Water Quality Monitoring and Assessment, Ohio Environmental Protection Agency, Columbus, Ohio.
- PALMER, M. A., A. E. BELY, AND K. E. BERG. 1992. Response of invertebrates to lotic disturbance: a test of the hyporheic refuge hypothesis. *Oecologia* (Berlin) 89:182-194.
- PARSONS, M., AND R. H. NORRIS. 1996. The effect of habitat-specific sampling on biological assessment of water quality using a predictive model. *Freshwater Biology* 36:419-434.
- PLAFKIN, J. L., M. T. BARBOUR, K. D. PORTER, S. K. GROSS, AND R. M. HUGHES. 1989. Rapid bioassessment protocols for use in streams and rivers. Benthic macroinvertebrates and fish. EPA 440-4-89-001. Office of Water Regulations and Standards, US Environmental Protection Agency, Washington, DC.
- RADER, R. B., AND J. V. MCARTHUR. 1995. The relative importance of refugia in determining the drift and habitat selection of predaceous stoneflies in a sandy-bottomed stream. *Oecologia* (Berlin) 103:1-9.
- RAMIREZ, A., P. PAABY, C. M. PRINGLE, AND G. AGUERO. 1998. Effect of habitat type on benthic macroinvertebrates in two lowland tropical streams, Costa Rica. *Revista de Biología Tropical* 46:201-213.
- REMPEL, L. L., J. S. RICHARDSON, AND M. C. HEALEY. 1999. Flow refugia for benthic macroinvertebrates during flooding of a large river. *Journal of the North American Benthological Society* 18:34-48.
- RICHARDS, C., AND K. L. BACON. 1994. Influence of fine sediment on macroinvertebrate colonization of surface and hyporheic stream substrates. *Great Basin Naturalist* 54:106-113.
- ROSENBERG, D. M., AND A. P. WIENS. 1978. Effects of sediment addition on macrobenthic invertebrates in a northern Canadian stream. *Water Research* 12:753-763.
- ROSENFELD, J. S., AND J. J. HUDSON. 1997. Primary production, bacterial production, and invertebrate biomass in pools and riffles in southern Ontario streams. *Archiv für Hydrobiologie* 139:301-316.
- ROY, A. H., A. D. ROSEMOND, M. J. PAUL, D. S. LEIGH, AND J. B. WALLACE. 2003. Stream macroinvertebrate response to catchment urbanization (Georgia, USA). *Freshwater Biology* 48:329-346.
- SEDELL, J. R., G. H. REEVES, F. R. HAUER, J. A. STANFORD, AND C. P. HAWKINS. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management* 14:711-724.
- STAMEY, T. C., AND G. W. HESS. 1993. Techniques for estimating magnitude and frequency of floods in rural basins of Georgia. US Geological Survey WRIR 93-4016. US Geological Survey, Atlanta, Georgia.
- STRAND, M., AND R. W. MERRITT. 1999. Impacts of livestock grazing activities on stream insect communities and the riverine environment. *American Entomologist* 45:13-29.
- SWANSON, F. J., S. L. JOHNSON, S. V. GREGORY, AND S. A. ACKER. 1998. Flood disturbance in a forested mountain landscape. *BioScience* 48:681-689.
- TOWNSEND, C. R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8:36-50.
- TRIMBLE, S. W. 1997. Contribution of stream channel erosion to sediment yield from an urbanizing watershed. *Science* 278:1442-1444.
- USDA (US Department of Agriculture). 2000. 1997 National Resource Inventory. Changes in land cover/use between 1982 and 1997. (Available from: http://www.nrcs.usda.gov/technical/NRI/1997/summary_report/table5.html)
- WALLACE, J. B., J. W. GRUBAUGH, AND M. R. WHILES. 1996. Biodiversity and coarse woody debris in southern forests. Pages 119-129 in J. W. McMinn and D. A. Crossley (editors). Influences of coarse woody debris on stream habitats and invertebrate biodiversity. General Technical Report SE-94. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. Meeting held in Athens, Georgia, 18-20 October 1993. US Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina.
- WANG, L. Z., J. LYONS, P. KANEHL, AND R. GATTI. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries* 22(6):6-12.
- WATERS, T. F. 1969. Subsampling for dividing large samples of stream invertebrate drift. *Limnology and Oceanography* 14:813-815.
- WATERS, T. F. 1995. Sediment in streams: sources, biological effects and control. *American Fisheries Society Monograph* 7. American Fisheries Society, Bethesda, Maryland.
- WIGGINS, G. B. 1996. Larvae of the North American caddisfly genera (Trichoptera). 2nd edition. University of Toronto Press, Toronto, Ontario.
- WOLMAN, M. G., AND A. P. SCHNICK. 1967. Effects of construction on fluvial sediment, urban and suburban areas of Maryland. *Water Resources Research* 3:451-464.
- WOOD, P. J., AND P. D. ARMITAGE. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* 21:203-217.

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APPENDIX. Insect taxa found at the 29 study sites and their habitat preferences. Rare taxa (i.e., only found at 1 site for each habitat) are excluded.

Taxon	Total density (no./m ²) ^a	Habitat pre- ference ^b
Ephemeroptera		
Ameletidae		
<i>Ameletus</i> spp.	12	B
Baetidae		
<i>Baetis</i> spp.	1056	F
Baetiscidae		
<i>Baetisca</i> spp.	14	F
Ephemerellidae		
<i>Drunella</i> spp.	22	R
<i>Ephemerella</i> spp.	4594	F
<i>Eurylophella</i> spp.	126	F
Caenidae		
<i>Caenis</i> spp.	<1	B
Ephemeridae		
<i>Hexagenia</i> spp.	661	F
Heptageniidae		
<i>Epeorus</i> spp.	229	R
<i>Rithrogena</i> spp.	184	R
<i>Stenomena</i> spp.	2596	F
Isonychidae		
<i>Isonychia</i> spp.	204	F
Leptophlebiidae		
<i>Leptophlebia</i> spp.	<1	B
<i>Paraleptophlebia</i> spp.	34	F
Odonata		
Zygoptera		
Calopterygidae		
<i>Calopteryx</i> spp.	9	B
Coenagrionidae		
<i>Argia</i> spp.	18	F
Anisoptera		
Aeshnidae		
<i>Boyeria</i> spp.	1	B
Cordulegastridae		
<i>Cordulegaster</i> spp.	5	B
Corduliidae		
<i>Macromia</i> spp.	8	B
Gomphidae		
<i>Ereptogomphus</i> spp.	5	R
<i>Gomphus</i> spp.	70	F
<i>Progomphus</i> spp.	26	B ^c

APPENDIX. Continued.

Taxon	Total density (no./m ²) ^a	Habitat pre- ference ^b
Plecoptera		
Chloroperlidae		
<i>Suwallia/Sweltsa</i> spp.	236	F
Nemouridae		
<i>Amphinemura</i> spp.	25	F
<i>Ostrocerca</i> spp.	93	F
Perlodidae		
<i>Acroneuria</i> spp.	54	F
<i>Eccoptura</i> spp.	5	B
<i>Neoperla</i> spp.	82	F
<i>Paragnetina</i> spp.	5	F
<i>Perlesta</i> spp.	293	F
Perlidae		
<i>Clioperla</i> spp.	<1	B
<i>Helopicus</i> spp.	19	R
<i>Isoperla</i> spp.	341	F
Peltoperlidae		
<i>Tallaperla</i> spp.	<1	B
Pteronarcyidae		
<i>Pteronarcys</i> spp.	53	F
Coleoptera		
Dryopidae		
<i>Helichus</i> spp.	51	F
Dytiscidae		
<i>Hygrotus</i> spp.	<1	B
Elmidae		
<i>Ancyronyx</i> spp.	47	F
<i>Dubiraphia</i> spp.	65	F
<i>Gonielmis</i> spp.	12	B
<i>Macronychus</i> spp.	<1	B
<i>Optioservus</i> spp.	1157	F
<i>Oulimnius</i> spp.	142	F
<i>Promoresia</i> spp.	8	R
<i>Stenelemis</i> spp.	342	F
Unidentified	9	R
Gyrinidae		
<i>Dineutus</i> spp.	7	B
<i>Gyrinus</i> spp.	<1	B
Heliplidae		
<i>Peltodytes</i> spp.	<1	B
Hydrophilidae		
<i>Enochrus</i> spp.	<1	B
Unidentified	<1	B

APPENDIX. Continued.

Taxon	Total density (no./m ²) ^a	Habitat pre- ference ^b
Psephenidae		
<i>Ectopria</i> spp.	9	B
<i>Psephenus</i> spp.	233	R ^d
Ptilodactylidae		
<i>Anchytarsus</i> spp.	40	F
Scirtidae		
<i>Scirtes</i> spp.	1	B
Staphylinidae		
<i>Stenus</i> spp.	2	B
Hemiptera		
Veliidae		
<i>Microvelia</i> spp.	6	B
Megaloptera		
Corydalidae		
<i>Corydalus</i> spp.	76	F
<i>Nigronia</i> spp.	9	B
Sialidae		
<i>Sialia</i> spp.	6	B
Diptera		
Athericidae		
<i>Atherix</i> spp.	10	F
Blephariceridae		
<i>Blepharicera</i> spp.	13	R
Ceratopogonidae		
<i>Atrichopogon</i> spp.	<1	B
<i>Ceratopogoninae</i> spp.	2568	F
Chironomidae		
Tanypodinae	64	F
Non-Tanypodinae	30,496	F
Dixidae		
<i>Dixa</i> spp.	36	F
Dolichopodidae		
Unidentified	10	B
Empididae		
<i>Chelifera</i> spp.	161	F
<i>Hemerodromia</i> spp.	476	F
Simuliidae		
<i>Simulium</i> spp.	1422	F
Stratiomyidae		
<i>Nemotelus</i> spp.	543	R
Tabanidae		
<i>Tabanus</i> spp.	39	F

APPENDIX. Continued.

Taxon	Total density (no./m ²) ^a	Habitat pre- ference ^b
Tipulidae		
<i>Antocha</i> spp.	270	F
<i>Dicranota</i> spp.	3	B
<i>Hexatoma</i> spp.	687	F
<i>Molophilus</i> spp.	64	B
<i>Tipula</i> spp.	38	F
Tanyderidae		
Unidentified	18	R ^d
Trichoptera		
Brachycentridae		
<i>Barchycentrus</i> spp.	99	F
Glossosomatidae		
<i>Glossosoma</i> spp.	63	R
Hydroptilidae		
<i>Ochrotrichia</i> spp.	96	F
Hydropsychidae		
<i>Cheumatopsyche</i> spp.	1279	F
<i>Hydropsyche</i> spp.	492	F
Limnephilidae		
<i>Ironoquia</i> spp.	<1	B
<i>Pycnopsyche</i> spp.	47	F
Philopotamidae		
<i>Chimarra</i> spp.	66	R
Polycentrophodidae		
<i>Polycentropus</i> spp.	<1	B
Psychomyiidae		
<i>Lype</i> spp.	19	F
<i>Psychomyia</i> spp.	18	R
Rhyacophilidae		
<i>Rhyacophila</i> spp.	15	R

^a Sum of habitat-weighted densities added across sites

^b Based on where taxa were found in this study. R indicates exclusive to riffle habitats, B indicates exclusive to bank habitats, and F indicates facultative (found in riffle, bank, and pool habitats)

^c Taxon found in bank and pool habitats

^d Taxa found in riffle and pool habitats