

# Reach-scale effects of riparian forest cover on urban stream ecosystems

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**Abstract:** We compared habitat and biota between paired open and forested reaches within five small streams (basin area 10–20 km<sup>2</sup>) in suburban catchments (9%–49% urban land cover) in the Piedmont of Georgia, USA. Stream reaches with open canopies were narrower than forested reaches (4.1 versus 5.0 m, respectively). There were no differences in habitat diversity (variation in velocity, depth, or bed particle size) between open and forested reaches. However, absence of local forest cover corresponded to decreased large wood and increased algal chlorophyll *a* standing crop biomass. These differences in basal food resources translated into higher densities of fishes in open (9.0 individuals·m<sup>-2</sup>) versus forested (4.9 individuals·m<sup>-2</sup>) reaches, primarily attributed to higher densities of the herbivore *Campostoma oligolepis*. Densities of terrestrial invertebrate inputs were higher in open reaches; however, trends suggested higher biomass of terrestrial inputs in forested reaches and a corresponding higher density of terrestrial prey consumed by water column feeding fishes. Reach-scale biotic integrity (macroinvertebrates, salamanders, and fishes) was largely unaffected by differences in canopy cover. In urbanizing areas where catchment land cover drives habitat and biotic quality, management practices that rely exclusively on forested riparian areas for stream protection are unlikely to be effective at maintaining ecosystem integrity.

**Résumé :** Nous avons comparé les habitats et les organismes vivants dans des sections appariées, boisées et ouvertes, dans cinq petits ruisseaux (surface du bassin 10–20 km<sup>2</sup>) dans des bassins versants de banlieue (9–49 % d'utilisation urbaine des terres) dans le piémont de Géorgie, É.-U. Les sections ouvertes de ruisseau sont plus étroites que les sections boisées (4,1 m vs 5,0 m, respectivement). Il n'y a pas de différence de diversité des habitats (variation de vitesse de courant, profondeur, granulométrie du lit) entre les sections ouvertes et boisées. Cependant, l'absence de couverture forestière locale entraîne une diminution de la quantité de bois de grande taille et une augmentation de la biomasse de chlorophylle *a* des algues. Ces différences de ressources alimentaires de base amènent des densités plus élevées de poissons dans les sections ouvertes (9,0 individuels·m<sup>-2</sup>) que dans les sections boisées (4,9 individuels·m<sup>-2</sup>), ce qui s'explique par des densités plus grandes de l'herbivore *Campostoma oligolepis*. La densité des apports d'invertébrés terrestres est plus grande dans les sections ouvertes; par contre, les tendances indiquent une biomasse plus grande des apports terrestres dans les sections boisées et une densité correspondante plus élevée de proies terrestres consommées par les poissons qui se nourrissent dans la colonne d'eau. L'intégrité biotique (macroinvertébrés, salamandres, poissons) au niveau des sections est généralement peu affectée par la couverture végétale. Dans les zones urbanisées où la couverture du sol du bassin versant détermine la qualité de l'habitat et de la communauté, les méthodes de gestion qui se basent exclusivement sur les zones ripariennes boisées comme moyen de protection des cours d'eau risquent de ne pas réussir à maintenir l'intégrité de l'écosystème.

[Traduit par la Rédaction]

## Introduction

Over the past two decades, research has highlighted the importance of riparian corridors as critical areas of the landscape for influencing stream ecosystem processes and stream biotic integrity (Correll 2000). These streamside areas have been labeled buffers because of their capacity to take up or

retain nutrients (Peterjohn and Correll 1984; Osborne and Kovacic 1993), sediments (Davies and Nelson 1994; Waters 1995), metals, and other contaminants (also see reviews in Gregory et al. 1991; Sweeney 1992; Lowrance 1998). Forested riparian corridors also provide bank and geomorphic stability, large woody debris, and other detrital inputs (Trotter 1990) and terrestrial arthropod inputs (Mason and Mac-

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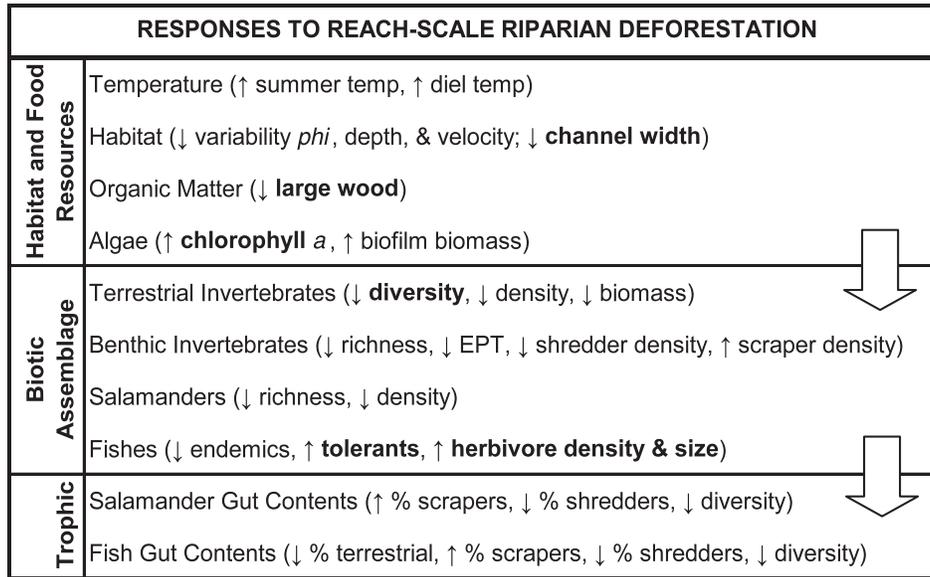
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**Fig. 1.** Conceptual model of relationships between reach-scale riparian deforestation and responses of basal food resources and consumers in urban streams. Riparian deforestation is predicted to result in changes in habitat (e.g., temperature and habitat diversity) and food resources (e.g., organic matter inputs and algae). We predict corresponding changes in biotic assemblages, including terrestrial invertebrates, benthic invertebrates, salamanders, and fishes. For example, reductions in terrestrial-derived carbon and increases in autochthonous carbon are predicted to increase densities of algae-eating invertebrates and fishes and decrease densities of shredding insects. We hypothesize that these changes in basal food resources will also be translated into differences in the proportions of prey types consumed by salamanders and fishes between open and forested reaches. Responses in bold indicate significant effects observed in this study.



Donald 1982; Kawaguchi and Nakano 2001). For streams in forested landscapes, removal of riparian forests decreases shading, increases temperature (Beschta and Taylor 1988), and increases primary productivity (Murphy et al. 1981; Noel et al. 1986), which influences the biotic communities by favoring certain species and altering population dynamics (Barton et al. 1985; Feminella et al. 1989). Many studies have demonstrated how structural habitat provided by riparian buffers indirectly affects higher trophic levels such as macroinvertebrates (Benke et al. 1988; Whiles et al. 2000) and fishes (Karr and Schlosser 1978; Jones et al. 1999). Essentially, forested riparian areas supply streams with a high diversity and quality of instream habitat for aquatic biota.

Although intact riparian corridors have been shown to minimize degradation of water quality and biotic integrity resulting from catchment land use disturbance, this research has primarily been conducted in watersheds with agricultural (e.g., Peterjohn and Correll 1984; Osborne and Kovacic 1993) and silvicultural (e.g., Beschta and Taylor 1988; Davies and Nelson 1994) land uses. Very little is known about the function of riparian forests in urban and suburban areas (but see Hession et al. 2003; Sweeney et al. 2004). We anticipate that riparian forests may not be sufficient to protect streams in urban settings because (i) these corridors are often bypassed by stormwater conveyances and (ii) the instream impacts of urban land cover in the catchment (e.g., owing to hydrologic alteration and increased pollutant delivery) are overwhelming. However, at the reach scale, forested riparian areas may still provide essential functions of shading, bank stability, and organic matter inputs for streams.

This study directly addressed the influence of reach-scale (200 m) riparian forests on habitat and biota in urbanizing streams. We compared water quality, physical habitat, food resources (e.g., algae), benthic and terrestrial invertebrates, salamanders, and fishes between paired open and forested reaches within five urban streams. We illustrated the predicted changes associated with reach-scale riparian deforestation (Fig. 1). Although riparian forests have been shown to reduce nutrient and sediments inputs to streams, we did not expect differences in water quality between adjacent open and forested reaches because of the close proximity of the reaches. Stream reaches without forested canopies are hypothesized to have higher mean annual temperature and temperature variability (Beschta and Taylor 1988; Sweeney 1992), reduced habitat diversity (e.g., variation in depth, velocity, and bed sediment size; Jones et al. 1999), reduced channel width (Davies-Colley 1997; Scarsbrook and Halliday 1999; Sweeney et al. 2004), reduced organic matter (Sweeney 1992), and increased algae (McIntyre and Phinney 1965). We also hypothesize that streams with lower canopy cover will have lower diversity, density, and biomass of terrestrial invertebrate inputs (Mason and MacDonald 1982; Edwards and Huryn 1996; Kawaguchi and Nakano 2001). Differences in habitat quality are expected to translate into differences in assemblage integrity of benthic macroinvertebrates, salamanders, and fishes. Shifts from allochthonous to autochthonous food resources with riparian deforestation are expected to result in decreased densities of shredding invertebrates dependent on leaf material (Wallace et al. 1999) and increased densities of herbivorous invertebrates (e.g., scrapers) and fishes. The relative changes in benthic and terrestrial invertebrates

**Table 1.** Site characteristics for study streams within the Etowah River basin, Georgia.

	Clark	Copper Sandy	Lawrence	Picketts Mill	Westbrook
<b>Location</b>					
UTM Northing (NAD 1983)	717 590	746 302	701 124	708 236	707 590
UTM Easting (NAD 1983)	3 773 997	3 777 695	3 758 149	3 761 223	3 770 001
County	Cobb/Cherokee	Fulton	Paulding	Cobb/Paulding	Paulding/Cobb
<b>Open reach</b>					
Type of land use	Golf course	Horse/cow pasture	Ball fields	Horse pasture	Golf course
Location (relative to forest reach)	Upstream	Downstream	Downstream	Upstream	Downstream
Total length open (m)	554	350	348	368	400
<b>Canopy cover (July 2002)</b>					
Open reach (%)	10.6	44.2	62.8	23.0	20.8
Forest reach (%)	91.3	82.1	96.1	83.8	58.9
<b>Basin and stream morphometry</b>					
Drainage area (km <sup>2</sup> )	16.2	16.0	11.8	15.1	18.9
Stream length (km)	36.9	34.2	24.4	34.1	46.2
Drainage density (km·km <sup>-2</sup> )	2.3	2.1	2.1	2.3	2.4
Elevation (m)	860	980	880	900	740
Stream slope	0.0034	0.0054	0.0035	0.0039	0.0034
<b>Catchment land cover</b>					
Impervious (%)	17.3	14.5	9.7	13.2	8.8
Urban (%)	49.3	20.5	8.8	25.6	19.5
Forest (%)	40.5	55.1	73.9	61.0	69.3
Agriculture (%)	3.5	13.0	9.1	7.8	4.2
Open water (%)	0.7	1.9	1.1	0.4	0.7
<b>Riparian land cover (network)</b>					
Urban (%)	16.3	5.5	2.9	8.3	2.4
Forest (%)	68.9	76.1	86.6	84.4	87.5
Agriculture (%)	2.3	8.8	5.3	3.8	6.1
Open water (%)	3.2	8.1	4.3	2.8	3.6
Road crossings (no.·km stream <sup>-1</sup> )	0.51	0.26	0.61	0.47	0.19
Impoundments (no.·km stream <sup>-1</sup> )	0.46	0.55	0.29	0.53	0.28

**Note:** Catchment land cover is based on 2001 Landsat Thematic Mapper satellite imagery. Riparian land cover is based on 1999 orthorectified aerial photographs. Reclassification of land cover subsequent to site selection (2001 versus 1997 data) resulted in <15% urban land cover in Lawrence Creek.

are expected to translate into diet shifts of insectivorous salamanders and fishes. Finally, we expected differential use of open and forest patches by small and large fish owing habitat availability, food availability, and (or) biotic interactions. Specifically, we hypothesized that herbivorous fishes would be larger in open reaches, reflecting higher growth rates owing to algal availability (Fig. 1). We tested these predicted differences between open and forested reaches to determine the function of reach-scale riparian forests in urban streams.

## Methods

### Study sites

This study took place in five small streams within the Piedmont physiographic region of the Etowah River basin, a 4823-km<sup>2</sup> catchment in north-central Georgia, USA. The region was originally dominated by deciduous forests; however, human practices in the last century have transformed the landscape into a mosaic of secondary forest, agriculture, and urban uses. In the last two decades, suburban development spreading from metropolitan Atlanta (population >4 million) has led to concerns of habitat degradation and species loss within the watershed (Burkhead et al. 1997).

Specifically, catchments of small streams (basin area 10–20 km<sup>2</sup>, approximately second to third order) within the Etowah River basin exhibited an average 13% decrease in forest cover and 11% increase in urban land cover between 1973 and 1997 (Roy et al. 2003a). Although on average, 1997 forest land cover was 5% higher in 100-m riparian corridors relative to the entire catchment, riparian areas also exhibited a 10% loss of forest cover and an 8% increase in urban land cover over the 24-year period (Roy et al. 2003a).

Five streams (Clark, Copper Sandy, Lawrence, Picketts Mill, and Westbrook Creeks) with paired sites in open and forested reaches (for a total of 10 sites) were selected for the study (Table 1). Streams were selected to be of similar size (drainage area from 10 to 20 km<sup>2</sup>) and similar slope (ranging from 0.34% to 0.54%). We selected streams in catchments that had >15% urban land cover (i.e., above the level at which effects of urban disturbance on biota should be detectable; Schueler 1994) and <30% agriculture land cover based on 1997 Landsat Thematic Mapper satellite imagery. Open reaches consisted of at least 200 m of stream that had an open canopy because of lack of forest on at least one side of the stream. Forested reaches had at least a 30-m width of forest on each side of the stream for the entire 200-m-long

reach. Less than 1 km of stream separated paired open and forested reaches and no significant tributaries entered between the paired reaches that would drastically change drainage area or upstream land cover. These five streams were the only streams with paired open and forested reaches that fit the design criteria within the Etowah River basin.

### Landscape assessment

Subsequent to site selection, we recalculated land cover for each subcatchment with 2001 Landsat Thematic Mapper satellite imagery (30-m pixels) because this was the most recent and applicable coverage available. We also determined land cover types within a 30-m-wide buffer (corresponding to typical lot widths) for the drainage network upstream of the sample site using 1999 orthorectified aerial photography (1-m resolution). Land cover was classified as urban (low and high density), forest (evergreen, deciduous, and mixed), agriculture (cultivated/exposed land, and cropland/grassland), open water, or other (e.g., clearcut and golf course). We determined percent impervious cover for each subcatchment from a classified data set created by the Georgia Land Use Trends Project (Natural Resources Spatial Analysis Laboratory, Institute of Ecology, University of Georgia, Athens, GA 30602, USA). Department of Transportation road data from 1999 were used to calculate the number of road crossings per stream length for each site. Air photographs from 1999 were also used to count the number of stream impoundments, which was divided by stream length for comparison across streams.

Percent canopy cover was measured at the stream centerline at 10 locations along each reach in July 2002 using a spherical densiometer. At 10 random transects (corresponding to terrestrial invertebrate input transects), we measured distance from stream bank and diameter at breast height for all trees within a 5-m-wide corridor extending 30 m from the stream bank. Tree density (number of trees per square metre), mean tree diameter, and basal area of trees per hectare were calculated from tree measurements.

### Environmental variables

Stream water chemistry was sampled five times from 7 November 2001 to 31 August 2002. Dissolved oxygen was measured with a portable Hydrolab Datasonde™ 4 (Hydrolab Corporation, Austin, Texas), which was calibrated before each use. Turbidity was measured in the field with a Hach™ turbidimeter (HACH Company, Loveland, Colorado). Grab water samples (taken halfway between bed and water surfaces) were filtered (Gelman® glass fiber, 0.45 µm; Gelman Sciences, Ann Arbor, Michigan) into acid-washed bottles, placed on ice, and transported to the laboratory for NH<sub>4</sub>-N, NO<sub>2</sub>/NO<sub>3</sub>-N, and soluble reactive P analysis using an Alpkem autoanalyzer (Alpkem Corporation, Wilsonville, Oregon) following standard methods protocol (American Public Health Association et al. 1989). We also calculated the molar ratio of dissolved N:P as dissolved inorganic N (NH<sub>4</sub>-N + NO<sub>2</sub>/NO<sub>3</sub>-N) to soluble reactive P. Hobo™ temperature data loggers were installed in November 2001 and stream temperature was recorded every 15 min for 1 year.

Stream slope was measured at the water surface at tops of riffles with a TopCon™ survey scope and stadia rod for the

200-m reach. Percentages of riffle, pool, and run habitat were calculated based on visual designation of habitat units determined by professional judgment using depth, water surface, and bed texture. A visual estimate of percent fines and percent embeddedness was made in one random location within each habitat unit using a view box. Depth, velocity, and modal particle size ( $\phi$ ) were measured at 34 random distances (68 for centerline) in the 200-m reach along five longitudinal transects (10, 30, 50, 70, and 90 percentiles) in a zigzag manner for a total of 204 measurements. These variables were used to calculate the Shannon index ( $H'$ ) (Zar 1974) as a measure of habitat diversity for single variables and all combinations of depth, velocity, and particle size (following Jones et al. 1999). A measure of evenness ( $J'$ ) (relative diversity) was also calculated by dividing  $H'$  by the log of the number of variable categories (1–3; Zar 1974). A quantitative estimate of percent fines (<2 mm) in riffle habitats was obtained by taking three 1-L grab samples of the bed sediment and dry sieving and weighing the material in the laboratory.

### Basal food resources

The amount of wetted large wood was measured for each 200-m sample reach. Diameter and length were measured for all submerged wood  $\geq 10$  cm in diameter and  $\geq 1$  m long to calculate total volume of large wood.

Biofilm and algal chlorophyll *a* were sampled during September–October 2003 during leaf-out at 10 equally spaced transects along the 200-m reach. Three samples were taken from the dominant substrate at each transect using a 60-mL syringe modified into a Loeb sampler (rock substrates) or sediment core (sand substrates). Samples were brought back to the laboratory on ice where sand samples were sonicated for 1 min. All samples were stirred for ~1 min and subsamples of a known volume of slurry were filtered onto Whatman® GF/F filters (Whatman Inc., Clifton, New Jersey) for chlorophyll *a* and biofilm biomass. Biofilm biomass samples were dried, ashed, and weighed to determine biofilm ash-free dry mass. Chlorophyll *a* was extracted from frozen filters by first cutting and grinding in 90% acetone to break apart any blue-green cells (adapted from Wetzel and Likens 1991). Samples were decanted into a centrifuge tube and placed in a refrigerator for ~24 h. Samples were then centrifuged for ~5 min, subsampled (if necessary), and analyzed for chlorophyll *a* with a fluorometer (TD-700; Turner Designs, Sunnyvale, California).

### Invertebrates

Benthic invertebrates were sampled in five replicate riffle habitats (one sample per riffle) at each of the 10 study reaches between 8 and 15 April 2002 prior to most insect emergence. Invertebrates were collected using a 0.09-m<sup>2</sup> surber sampler (500-µm mesh) and scrubbing rocks to a depth of 10 cm for 3 min. Samples were elutriated in the field, separated into small (0.5–1 mm) and large (>1 mm) size fractions, and preserved in 10% formalin. In the laboratory, the small fraction was subsampled to 100 invertebrates using a wheel sample splitter when necessary. All invertebrates in the large fraction and the subsampled small fraction were counted and identified to genus except for Chirono-

midae (classified as predatory Tanypodinae or collector-gatherers) and noninsects (identified to order) using standard keys (Merritt and Cummins 1996). Richness (number of taxa), density (number of individuals per square metre), and other macroinvertebrate composition measures (Ephemeroptera, Plecoptera, and Trichoptera richness and functional feeding group densities) were calculated.

Terrestrial invertebrate inputs into the stream were sampled 8–16 July 2002. Invertebrates were collected by placing 10 floating clear containers (surface area = 0.344 m<sup>2</sup> each) filled with water and unscented soap (surfactant) at random transects along the stream reach (based on methods similar to those in Mason and MacDonald 1982). Invertebrates were removed after 24 h and preserved in formalin. In the laboratory, invertebrates were identified to order, counted, and dried to determine biomass. Diversity was calculated using the Shannon–Weiner diversity index  $H'$ .

### Salamanders

Stream reaches were surveyed for stream salamanders at the three streams with riffle habitat in both open and forested reaches during 30–31 March 2003. We used a backpack electrofisher (model 12-B; Smith-Root®, Inc., Vancouver, Washington) in leaf packs and shallow riffle areas while kicking rocks and organic debris and holding a 500- $\mu$ m-mesh kick net downstream. We searched for equal amounts of time in open and forested reaches within each stream and recorded shock time. Salamanders were euthanized using an overdose of tricaine methanesulfonate (MS 222), preserved in 10% formalin, and brought back to the laboratory for identification and gut analysis. Area (square metres) of riffle habitat sampled for salamanders was measured to estimate salamander densities.

In the laboratory, salamanders were transferred to 70% ethanol. Each individual was counted and measured for snout–vent length. Salamander stomach contents were analyzed for all individuals in Lawrence Creek (four total) and Picketts Mill Creek (27 total) and a randomly selected subset of 12 individuals within each reach at Clark Creek. We removed the stomachs and intestines of individuals under a dissecting microscope (15 $\times$  magnification). Gut contents were identified to lowest possible taxonomic unit (typically order or family) and counted. Salamander abundance, catch per unit effort time, diversity of prey items ( $H'$ ), and percent abundance of dominant food item were calculated for each reach.

### Fishes

In fall 2001, fish assemblages were sampled using a backpack electrofisher in the most efficient manner for the habitat present: a downstream seine was used for riffles, dip nets were used for deep pools, and seine hauls were used for shallow homogenous runs. Block nets were used to separate habitat units (riffle, riffle–run, pool, and pool–run) and each segment was fished for three passes. We sampled a minimum of three replicate riffle or riffle–run and pool or pool–run habitats for a total stream length of up to 200 m. Fishes were identified in the field, measured, and released. Individual fish that could not be identified (including young of the year) were euthanized using MS

222, preserved in 8% formalin, and brought to the laboratory for identification.

Fish data were used to calculate richness and density of various composition metrics. We assessed fish assemblage integrity with measures of tolerant species, habitat generalists, and cosmopolitan species (indicative of low assemblage integrity) and highland endemic species (indicative of high assemblage integrity). Tolerant species were defined as widespread ubiquitous species found in over 80% of small streams in the Etowah based on previous research (Walters et al. 2003) and are expected to be tolerant of multiple stressors (Appendix A). Habitat generalists were defined as species that do not show preference for pool, pool–run, or riffle–run habitats and were classified based on Etnier and Starnes (1993) and Mettee et al. (1996). Cosmopolitan species were defined as those fishes native to at least 10 major drainages, whereas endemic species were primarily limited to the Coosa River drainage (Walters et al. 2003). We also examined the ratio of endemics to cosmopolitans (based on species richness and abundance), a metric that should detect homogenization of fish assemblages coincident with a loss of endemic species (Scott and Helfman 2001; Walters et al. 2003). We assessed standard length of individuals to compare differences in fish size (as reflective of growth or year class) between open and forested reaches for all individuals and with young of the year (YOY) excluded.

Individuals of two invertivore species (blackbanded darter (*Percina nigrofasciata*) and Alabama shiner (*Cyprinella callistia*)) and two trophic generalist species (redbreast sunfish (*Lepomis auritus*) and Alabama hog sucker (*Hypentelium etowanum*)) collected during sampling in fall 2001 were brought back to the laboratory for gut content analysis. Coosa shiner (*Notropis xaenocephalus*), an invertivore, was collected instead of *C. callistia* at one site where the latter species was not encountered. In the laboratory, all individuals were measured and weighed and the contents of the stomachs and intestines were removed from the fishes. We identified the gut contents of a maximum of 10 individuals; if more than 10 individuals were collected, we selected individuals most similar in size between open and forested reaches at a stream. Gut contents were identified to the lowest possible taxonomic unit (typically order or family) and counted. Percent abundance of food types (at the level of order) and percent terrestrial (versus aquatic) food items were compared between open and forested reaches.

### Data analysis

This study was designed to compare reaches with different amounts of riparian cover, with all other land cover factors being equal. Thus, paired  $t$  tests were used to compare mean differences between open and forested reaches in environmental, basal food resource, algae, invertebrate, salamander, and fish variables. Fish lengths were compared using two-sample  $t$  tests (assuming unequal variances) for each species that had greater than four individuals in open and forested reaches. Because open and forested reaches exhibited a wide range in percent canopy cover, scatterplots and linear regressions ( $r^2$ ) were also used to assess environmental and biotic parameters relative to percent canopy cover. All percentage data were transformed using arcsine square

**Table 2.** Comparison of riparian cover, water quality, selected physical habitat variables, and algae and biofilm between open and forested reaches (paired *t* test for means, *df* = 4).

	Open		Forest		<i>t</i>	<i>p</i>
	Mean	SD	Mean	SD		
Riparian trees and canopy cover						
Canopy cover (%)	<b>32.3</b>	<b>21.0</b>	<b>77.6</b>	<b>12.5</b>	<b>4.73</b>	<b>0.005</b>
Tree density (no.·m <sup>-2</sup> ) <sup>a</sup>	<b>0.038</b>	<b>0.037</b>	<b>0.179</b>	<b>0.055</b>	<b>4.53</b>	<b>0.010</b>
Tree diameter (cm) <sup>a</sup>	22.2	12.3	11.6	2.6	1.68	0.096
Basal area (m <sup>2</sup> ) per hectare <sup>a</sup>	<b>108</b>	<b>80</b>	<b>482</b>	<b>212</b>	<b>3.66</b>	<b>0.018</b>
Water quality						
Baseflow discharge (m <sup>3</sup> ·s <sup>-1</sup> )	0.037	0.008	0.035	0.007	0.69	0.264
Dissolved oxygen (mg·L <sup>-1</sup> )	<b>9.4</b>	<b>1.0</b>	<b>8.9</b>	<b>1.0</b>	<b>2.51</b>	<b>0.033</b>
Turbidity (NTU)	12.8	9.2	10.8	4.7	0.82	0.229
SRP (µg·L <sup>-1</sup> )	0.008	0.010	0.005	0.003	0.52	0.315
NH <sub>4</sub> -N (µg·L <sup>-1</sup> )	0.005	0.007	0.003	0.004	0.92	0.206
NO <sub>2</sub> /NO <sub>3</sub> -N (µg·L <sup>-1</sup> )	<b>0.114</b>	<b>0.033</b>	<b>0.126</b>	<b>0.038</b>	<b>5.71</b>	<b>0.002</b>
DIN:SRP	92.1	158.9	18.3	11.8	0.91	0.215
Temperature						
Annual mean (°C) <sup>a</sup>	15.60	2.20	15.24	2.01	1.78	0.075
Annual daily diel (°C) <sup>a</sup>	4.34	0.98	3.55	0.70	1.43	0.113
Summer daily minimum (°C) <sup>a,b</sup>	<b>21.06</b>	<b>0.88</b>	<b>20.13</b>	<b>0.17</b>	<b>2.34</b>	<b>0.051</b>
Summer daily maximum (°C) <sup>a,b</sup>	27.13	1.85	25.86	1.35	1.15	0.166
Channel morphology						
Riffle area (%)	17.2	10.1	27.1	18.4	1.12	0.148
Width mean (m)	<b>4.1</b>	<b>1.2</b>	<b>5.0</b>	<b>1.1</b>	<b>2.12</b>	<b>0.051</b>
Depth mean (m)	0.22	0.08	0.25	0.12	0.46	0.334
Large wood						
Total no. of pieces	<b>10.0</b>	<b>5.1</b>	<b>31.8</b>	<b>17.6</b>	<b>2.92</b>	<b>0.022</b>
Total volume (m <sup>3</sup> )	0.4	0.4	1.3	1.3	1.51	0.103
Biofilm and algae						
Biofilm AFDM (g·m <sup>-2</sup> )	32.9	9.7	100.9	150.6	1.04	0.179
Chlorophyll <i>a</i> (mg·m <sup>-2</sup> )	<b>32.7</b>	<b>16.9</b>	<b>13.7</b>	<b>11.3</b>	<b>2.17</b>	<b>0.048</b>

**Note:** NTU, nephelometric turbidity units; DIN, dissolved inorganic nitrogen; SRP, soluble reactive phosphorus; AFDM, ash-free dry mass. Bold indicates  $p \leq 0.051$ .

<sup>a</sup>*df* = 3.

<sup>b</sup>Open reach of Clark Creek missing for 1 April to 26 June, replaced with forest data (i.e., conservative extrapolation); Westbrook data ended 11 June.

root, and abundance data were transformed using  $\log(x + 1)$  or  $x^{0.25}$  where necessary to normalize skewed distributions.

## Results

### Differences in environmental variables and basal food resources

Canopy cover at forested reaches (77.6%) was about twice that at open reaches (32.3%) (Table 2). Land cover adjacent to open reaches included golf courses, pasture, and ball fields (Table 1). Catchments upstream from our sites contained from 8.8% to 49.3% urban land cover (based on reclassification subsequent to site selection). Impervious cover in the catchments (9.7%–17.3%) and density of road crossings (0.19–0.61 m stream length<sup>-1</sup>) also reflected the urban influence on these streams (Table 1). Riparian vegetation differed between reaches, with higher densities of trees in forested reaches ( $p = 0.010$ ), although trees in open reaches tended to be larger in diameter than those in forested reaches (result not significant,  $p = 0.096$ ) (Table 2).

In general, water quality was similar between open and forested reaches (Table 2). One notable exception was dis-

solved oxygen, with higher daytime concentrations in open (9.4 mg·L<sup>-1</sup>) versus forested reaches (8.9 mg·L<sup>-1</sup>). Additionally, NO<sub>2</sub>/NO<sub>3</sub>-N concentrations were higher in forested reaches versus in open reaches. Differences in canopy cover between paired reaches also affected stream temperature, with higher summer daily minimum temperature and trends (although not significant) toward higher diel temperatures in open reaches (Table 2).

There were no significant differences in percent riffle area between open and forested reaches (Table 2). Although there were no differences in depth between reaches, streams were on average about 20% wider in forested (5.0 m) versus open reaches (4.1 m). We hypothesized that riparian deforestation would alter in-stream habitat diversity; however, we found no evidence of differences in diversity ( $H'$ ) or evenness ( $J'$ ) of depth, velocity, or bed sediment size or any combination of those variables ( $p = 0.31$ – $0.50$ ) (see Roy 2004). As expected, the number of large wood pieces was higher in forested reaches compared with open reaches, although there were no significant differences in volume of large wood (Table 2).

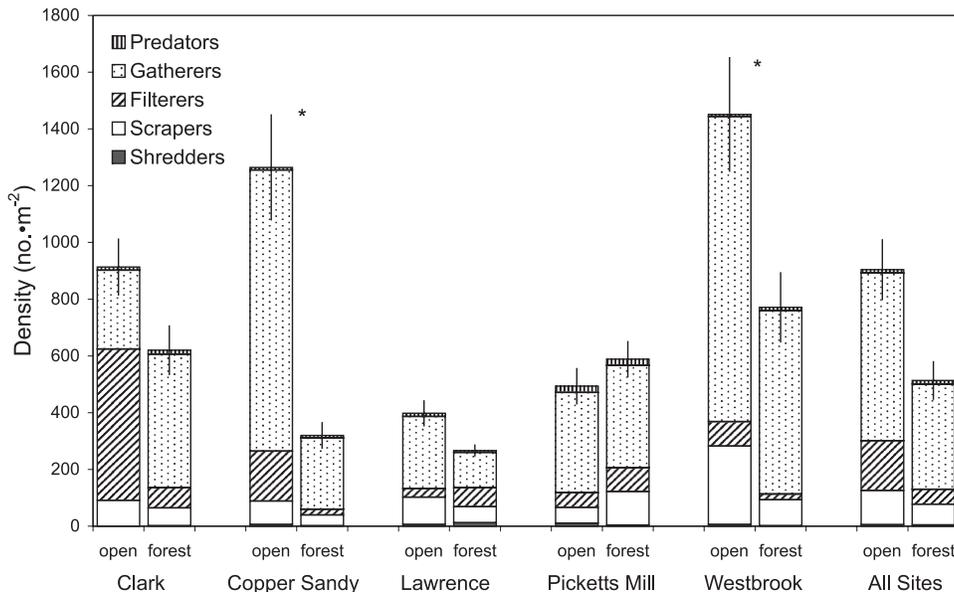
Higher light associated with open canopies was expected to result in higher amounts of benthic algae. Although there

**Table 3.** Comparison of benthic invertebrate (mean of five replicates per site,  $df = 4$ ) and total salamander ( $df = 2$ ) measures between open and forested reaches (paired  $t$  test for means).

	Open		Forest		$t$	$p$
	Mean	SD	Mean	SD		
<b>Benthic invertebrates</b>						
<b>Richness</b>						
Total richness	16.8	10.6	6.1	8.1	1.01	0.185
Insect richness	13.1	8.1	5.4	6.0	1.06	0.075
Ephemeroptera, Plecoptera, and Trichoptera richness	5.5	3.6	2.5	1.9	0.38	0.361
<b>Density</b>						
Total density (no.·m <sup>-2</sup> ) <sup>a</sup>	1131.5	822.3	633.8	535.4	1.75	0.077
SD total density (no.·m <sup>-2</sup> )	<b>586.8</b>	<b>447.1</b>	<b>378.4</b>	<b>292.2</b>	<b>2.74</b>	<b>0.026</b>
Scraper density (no.·m <sup>-2</sup> ) <sup>a</sup>	120.0	88.3	72.9	31.6	1.31	0.131
Shredder density (no.·m <sup>-2</sup> ) <sup>a</sup>	6.2	4.0	4.9	4.8	1.35	0.124
<b>Salamanders (<i>Eurycea cirrigera</i>)</b>						
Catch per unit effort	0.5	0.7	0.2	0.1	0.93	0.225
Snout-vent length (mm)	3.0	0.5	2.9	0.2	0.59	0.308
Stomach content density ( $H'$ )	1.2	0.8	1.3	0.5	0.64	0.294
Dominant food item abundance (%)	55.5	29.0	54.2	18.0	0.09	0.468

**Note:** Bold indicates  $p < 0.05$ .

<sup>a</sup> $\log(x + 1)$  transformed for analysis.

**Fig. 2.** Mean densities of benthic invertebrate functional feeding groups in open and forested reaches of each stream. Comparisons in overall mean densities between open and forested reaches within streams (two-sample  $t$  test assuming unequal variances,  $df = 4$ ) and among all stream pairs ("all sites", paired  $t$  test for means,  $df = 4$ ) are reported. Lines indicate  $\pm$  standard errors for overall mean densities. \*,  $p < 0.05$ .

was no significant difference in biofilm biomass between paired reaches (Table 2), biomass on rock substrates was marginally ( $p = 0.051$ ) higher in open versus forested reaches (Roy 2004). We also found significantly higher concentrations of chlorophyll  $a$  in open versus forested reaches.

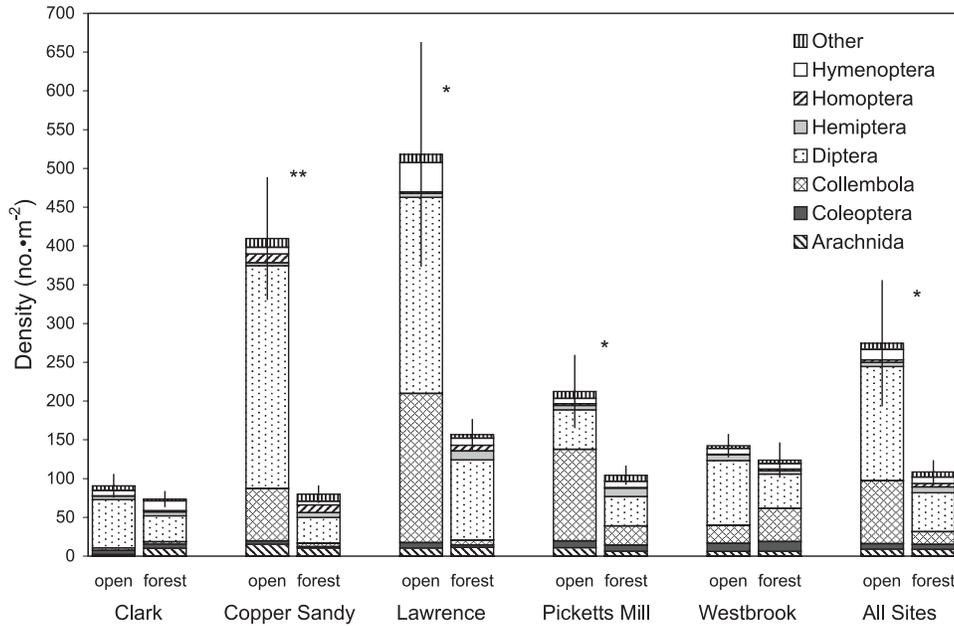
### Differences in biotic assemblages

Benthic invertebrates in riffle habitats did not differ in total taxa richness or richness of insect or Ephemeroptera, Plecoptera, and Trichoptera taxa (Table 3). In addition, there were no significant differences in benthic invertebrate densities between paired reaches, although most streams had higher insect densities in open versus forested reaches

(Fig. 2). The variation in densities among replicate samples (an indicator of patchiness) was significantly higher in open reaches compared with forested reaches. Scraper density (i.e., insects that primarily feed on benthic algae) was higher in open reaches compared with forested reaches in all sites except Picketts Mill Creek; however, the overall differences did not result in a significant effect of canopy cover. Shredders (i.e., insects that primarily feed on leaf material) accounted for a very small portion of the invertebrate density, and there were no differences in densities between reaches (Table 3; Fig. 2).

Terrestrial invertebrate inputs were numerically dominated by Diptera and Collembola at all sites (Fig. 3). We expected overall inputs to be higher in forested reaches, where insects

**Fig. 3.** Mean densities of common terrestrial invertebrate groups (mean density >1 m<sup>-2</sup>) in open and forested reaches of each stream. Comparisons in overall densities between open and forested reaches within streams (two-sample *t* test assuming unequal variances, *df* = 9) and among all stream pairs (“all sites”, paired *t* test for means, *df* = 4) are reported. Lines indicate ± standard errors for overall mean densities. \*, *p* < 0.05; \*\*, *p* < 0.01.



**Table 4.** Comparison between measures of fish assemblage composition and integrity between open and forested reaches (paired *t* test for means, *df* = 4).

	Open		Forest		<i>t</i>	<i>p</i>
	Mean	SD	Mean	SD		
<b>Overall measures</b>						
Species richness	16	2.9	14.8	3.0	1.63	0.089
Density (no.·m <sup>-2</sup> )	<b>9.0</b>	<b>2.4</b>	<b>4.9</b>	<b>1.7</b>	<b>4.78</b>	<b>0.004</b>
Relative abundance one dominant species	0.37	0.10	0.29	0.10	1.27	0.136
<b>Endemic (E) and cosmopolitan (C) species</b>						
Endemic richness	2	1	1.6	1.1	1.63	0.187
Endemic density (no.·m <sup>-2</sup> )	1.05	0.74	0.85	0.70	0.88	0.215
Cosmopolitan richness	<b>5.22</b>	<b>2.77</b>	<b>2.83</b>	<b>1.94</b>	<b>3.81</b>	<b>0.009</b>
Cosmopolitan density (no.·m <sup>-2</sup> )	8.6	1.1	8.2	1.8	1.00	0.187
E/(E + C) (abundance) <sup>a</sup>	0.16	0.11	0.24	0.21	1.64	0.088
<b>Gut content diversity (<i>H'</i>)</b>						
<i>Lepomis auritus</i>	0.19	0.01	0.20	0.01	1.56	0.096
<i>Cyprinella callistia</i>	0.07	0.07	0.17	0.02	1.82	0.105
<i>Percina nigrofasciata</i>	0.11	0.01	0.11	0.01	0.37	0.370
<i>Hypentelium etowanum</i>	0.11	0.02	0.11	0.01	0.04	0.484

**Note:** Invertebrate prey diversity was assessed in four species of fish. Bold indicates *p* < 0.05.

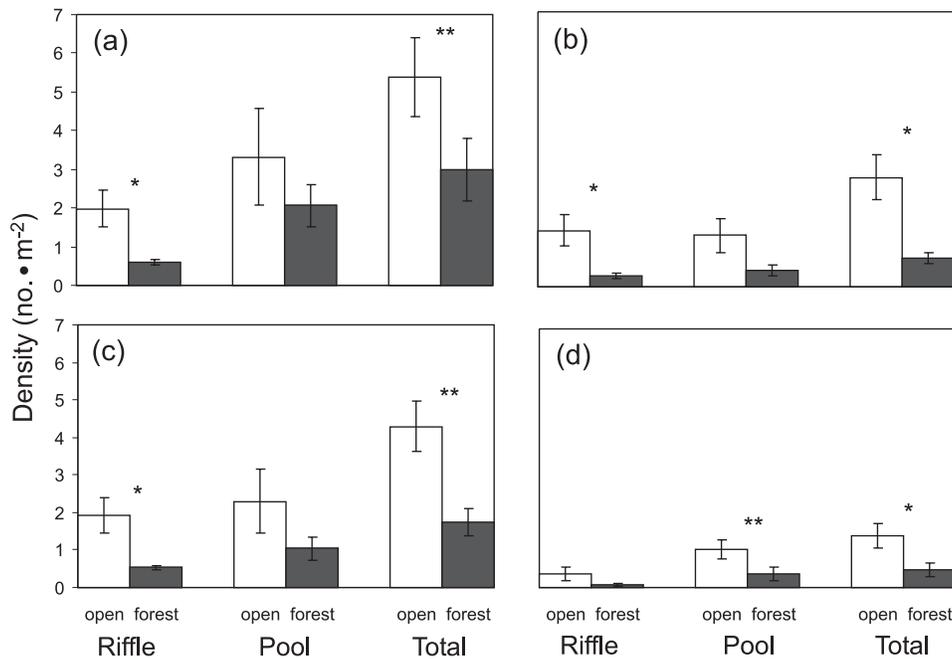
<sup>a</sup>Abundance *x*<sup>0.25</sup> transformed prior to calculating the ratio of E to C or E to E + C.

were more likely to fall from the canopy into stream reaches. Contrary to our expectation, there was a higher density of terrestrial invertebrates in open (275 individuals·m<sup>-2</sup>) versus forested reaches (108 individuals·m<sup>-2</sup>) (*p* = 0.048), primarily driven by higher densities of Diptera in open reaches (Fig. 3). In contrast, forested reaches had higher mean terrestrial invertebrate biomass (0.092 g·m<sup>-2</sup>) compared with open reaches (0.044 g·m<sup>-2</sup>), although the difference was not significant (*p* = 0.129). Forested reaches also exhibited a higher diversity of terrestrial invertebrate inputs

compared with open reaches (*H'* = 1.68 versus 1.28, *p* = 0.019).

The Southern two-lined salamander (*Eurycea cirrigera*) was the only salamander found at the three streams sampled, and all except three individuals were larvae. The catch per unit effort varied more across streams than between paired reaches, and there were no differences in salamander size between open and forested reaches (Table 3). Notably, at Clark Creek, a site with abundant cobble–gravel riffle habitat and highest salamander abundances, we captured 100 in-

**Fig. 4.** Densities (mean  $\pm$  1 SE) of tolerant fish species groups and the two most abundant fish species in riffle habitats, pool habitats, and all habitats combined. Comparisons between mean densities for open (open bars) and forested (solid bars) reaches are reported (paired *t* test for means, *df* = 4). \*, *p* < 0.05; \*\*, *p* < 0.01. (a) Tolerants; (b) *Campostoma oligolepis*; (c) habitat generalists; (d) *Fundulus stellifer*.



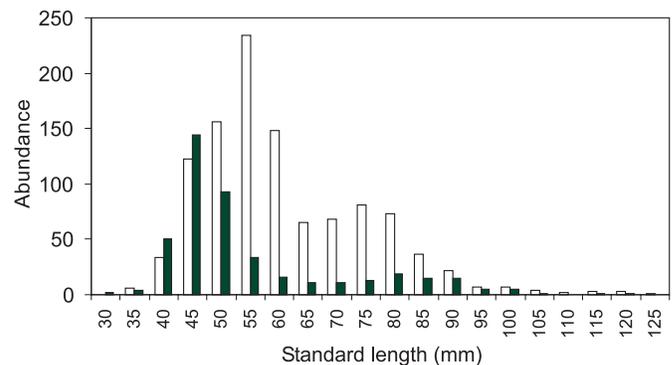
individuals in the open reach compared with 18 in the forested reach. Larval salamander gut contents revealed similar diversity of diets and percent abundance of dominant food items between open and forested reaches (Table 3).

There were significantly higher densities of fishes in open versus forested reaches (Table 4). These higher overall densities in open reaches were driven by higher densities of the largescale stoneroller (*Campostoma oligolepis*), an herbivore, and the southern sturgeon (*Fundulus stellifer*) (Fig. 4). These comparisons were consistent across habitat type; riffle habitats had higher *C. oligolepis* densities in open reaches, pool habitats had higher *F. stellifer* densities in open reaches, and no other fish group showed significant differences between reaches within habitat types (Fig. 4).

There were no differences in fish assemblage integrity in terms of species richness or dominance by one species (Table 4). Trends suggested a higher abundance of endemics relative to cosmopolitan species in forested reaches (difference not significant, *p* = 0.088). There was significantly higher richness of cosmopolitan species (Table 4) and density of tolerant and habitat generalist species (Fig. 4) in the open reaches relative to the forested reaches. However, these differences were driven primarily by higher densities of *C. oligolepis*, which is considered a cosmopolitan, tolerant, and habitat generalist species (Appendix A).

Four cyprinid fish species were significantly larger in forested reaches, and for all species except *C. callistia*, these differences were driven by YOY cyprinids collected in the open reach of Westbrook Creek (Appendix A). Black redhorse (*Moxostoma duquesnei*), bluegill (*Lepomis macrochirus*), and redear sunfish (*Lepomis microlophus*) were significantly larger in open reaches, potentially reflecting differences in

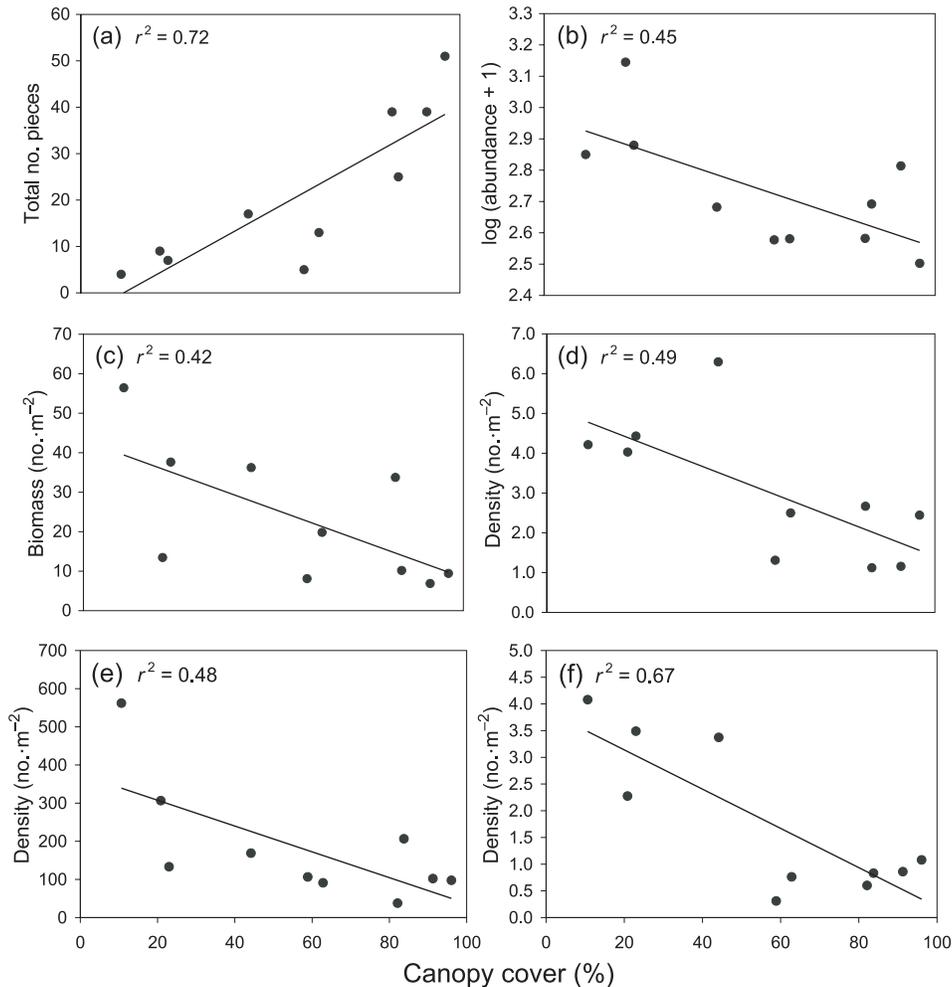
**Fig. 5.** Frequency histogram of abundances of *Campostoma oligolepis* in open (open bars) and forested (solid bars) reaches grouped by standard length of individual fish (combined for all five sites).



food resources. Conversely, speckled madtom (*Noturus leptacanthus*) and *P. nigrofasciata* were significantly larger in forested reaches. *Fundulus stellifer*, Coosa banded sculpin (*Cottus caroliniae zopherus*), and *L. auritus* were larger in forested reaches when YOY were included, and *H. etowanum* and speckled darter (*Etheostoma stigmaeum*) were larger in open reaches when YOY were excluded, suggesting that there were more YOY in open reaches for all five species (Appendix A). Size differences in *C. oligolepis* suggest that there were more, smaller individuals in open reaches, and for the first apparent age class, individuals were larger in open reaches than in forested reaches (Fig. 5).

Based on gut content analysis, we found no significant differences in the diversity of prey items in the guts of fish

**Fig. 6.** Linear regressions ( $r^2$ ) for selected environmental variables and percent canopy cover in 10 stream reaches: (a) large wood; (b) total fish species; (c) chlorophyll *a*; (d) habitat generalist fish species; (e) Ephemeroptera, Plecoptera, and Trichoptera invertebrate taxa; (f) herbivore fish species.



invertivores (*P. nigrofasciata* and *C. callistia*) or the trophic generalists (*L. auritus* and *H. etowanum*) (Appendix A). *Lepomis auritus* had higher proportional densities of dipteran pupae in open reaches (3.5% versus 0.5%, paired *t* test,  $p = 0.015$ ,  $n = 5$ ), higher arachnids in forested reaches (5.1% versus 3.4%,  $p = 0.03$ ), and a trend toward higher densities of terrestrial prey in forested reaches (54% versus 44%,  $p = 0.15$ ). Water column cyprinid fishes (*C. callistia*, two sites, and *N. xaenocephalus*, one site) contained over twice the proportional density of terrestrial prey in forested reaches (47% compared with 22% in open reaches,  $p = 0.106$ ). Although we hypothesized that fishes would consume a higher proportion of scraping insects in open reaches, differences of aquatic mayflies (Ephemeroptera, primarily scrapers) in gut contents between open and forested reaches were inconsistent across the fish species examined and not statistically significant (all  $p > 0.15$ ).

#### Relationships based on percent canopy cover

Although our site selection criteria resulted in clear differences between open and forested reaches within sites (smallest difference between canopy cover in open and forested

reaches was 33.3% in Lawrence Creek) (Table 1), there was a wide range in canopy cover in open (10.6%–62.8%) and forested reaches (58.9%–96.1%) across sites. Thus, we examined relationships between percent canopy cover and environmental and biotic variables to see if differences were better explained by the gradient of forest canopy cover. For the variables with data from all 10 sites, six were significantly explained by percent canopy cover ( $r^2 > 0.42$ ,  $p < 0.05$ ) (Fig. 6). Examination of scatterplots suggests that the amount of large wood is directly related to canopy cover within the reach ( $r^2 = 0.72$ ). However, percent canopy cover explains less than half of the variance (42%–48%) in chlorophyll *a*, Ephemeroptera, Plecoptera, and Trichoptera invertebrate density, and fish abundance, and observation of scatterplots verifies that canopy cover is not strongly driving these variables. The significant relationships between percent canopy cover and habitat generalist and herbivore fish species seem to be attributed to two separate groups with open (<50% cover) and forest canopies (>50% cover) (Fig. 6). In other words, except for Lawrence Creek where both reaches have relatively high forest cover, the difference in open and forest canopies in adjacent reaches within a

stream better explains differences in environmental and biotic variables.

## Discussion

### Changes in stream quality and integrity

Habitat diversity, a measure commonly used to evaluate stream quality, was remarkably unaffected by reach-scale riparian deforestation in our study, suggesting that habitat quality may be controlled by catchment-scale factors (e.g., land cover and hydrology) more than by reach-scale forest cover in these urbanizing streams. In fact, of 27 morphometric, bed texture, and habitat diversity (depth, velocity, and particle size) variables measured (Roy 2004), the only difference between reaches was in wetted width. Narrower channels in open (pasture) versus forested reaches have been found in several studies (Davies-Colley 1997; Scarsbrook and Halliday 1999; Sweeney et al. 2004); this is likely due to higher floodplain deposition rates relative to cutbank erosion in streams with grassy bank vegetation (Allmendinger et al. 2005). Because mean depth and baseflow discharge were not different between reaches, mean velocities were likely lower in forested reaches. Large wood is also important in structuring stream habitat, which was strongly explained by percent canopy cover, indicating that downstream transport of wood from forested to open reaches was not obscuring differences between reaches. Although local riparian deforestation may not eliminate large wood from stream systems, long-term reductions in supply might have an important influence on large wood volume and habitat complexity in urban streams.

Water quality was not expected to differ between open and forested reaches, since chemistry was assumed to be driven by catchment-scale factors such as urban and agriculture land cover and hydrologic alteration. Although most of the water quality variables did not differ between reaches, we measured higher amounts of daytime dissolved oxygen in open reaches. This difference is likely due to increased photosynthesis in open reaches that have higher amounts of primary producers. We also found higher concentrations of  $\text{NO}_2/\text{NO}_3\text{-N}$  in forested reaches. Although riparian zones are typically sinks for nitrate, Groffman et al. (2003) found that nitrification is increased in urban systems because of lowered water tables. Uptake of nitrogen by algae in open reaches may also be important in driving lower ambient  $\text{NO}_2/\text{NO}_3\text{-N}$  concentrations in open reaches. Local riparian deforestation increased summer minimum water temperatures by about 1 °C; however, we did not observe significant annual responses of temperature and temperature fluctuations to riparian deforestation. Longer openings in the riparian forest canopy are likely to alter stream temperatures more significantly, which may substantially impact fishes that cannot tolerate warmer temperatures (Scott and Helfman 2001).

Reach-scale biotic integrity was largely unaffected by local canopy cover. These streams had lower macroinvertebrate and Ephemeroptera, Plecoptera, and Trichoptera richness relative to other streams in the area; a random sample of 30 small (8–121 km<sup>2</sup>) Etowah streams sampled in 1999 averaged 15% urban land cover (compared with 24.7% in this study) and over nine Ephemeroptera, Plecoptera, and

Trichoptera species (compared with six in this study; Roy et al. 2003b). However, contrary to the expected reach-scale benefits of riparian forests to biotic integrity, we found no differences in macroinvertebrate assemblage integrity between open and forested reaches. This suggests that macroinvertebrate assemblages are likely driven more by catchment-scale factors (e.g., land cover) or reach-scale habitat quality than reach-scale forest cover. Salamander catches also did not differ based on forest cover, supporting the results of Hawkins et al. (1983) and Wilson and Dorcas (2003). Again, the reduced richness in these urban streams (only one species observed) may suggest that salamanders are primarily impacted by factors other than reach-scale riparian disturbance.

Total and endemic fish species richness did not indicate differences in fish assemblage integrity between reaches. Although fish assemblages had higher densities of tolerant and habitat generalist species in open reaches, these were driven by the abundance of two species (*C. oligolepis* and *F. stellifer*) and do not reflect an overall community shift in biotic integrity between reaches. The lack of response in biotic assemblages may be a consequence of minimal differences in habitat quality with reach-scale riparian deforestation. It is also possible that urban streams are already so depauperate of fishes that further changes in land cover would not affect the assemblage. However, our study streams supported 10–18 fish species, similar to fish richness (10–23) observed by Walters et al. (2003) in their 10 smallest Etowah streams. It is more likely that the high mobility of fishes and the presence of sufficient habitat and (or) thermal refugia in the sampled reach or adjacent reaches prevented severe local depletion of fish species. Given sufficient fish mobility, the open reaches could also be areas of “sink” fish populations supported by upstream or downstream forested areas (Gotelli and Taylor 1999; Jones et al. 1999).

### Changes in the trophic basis of production

Reach deforestation resulted in reduced organic inputs into the stream. On average, the open reaches had one fifth the amount of trees compared with forested reaches, which is expected to translate into a significant reduction in leaf inputs. For example, in a study looking at the effects of forest clearcutting on a headwater stream in North Carolina, tree basal area was reduced from 23.7 to 7.9 m<sup>2</sup>·ha<sup>-1</sup> (Elliot et al. 1997), and there was a concomitant reduction in litterfall (259.2–4.2 g·m<sup>-2</sup>) and blow-in (174.8–38.6 g·m<sup>-1</sup>) inputs to the stream (Webster and Waide 1982). We also found a direct relationship between canopy cover and large wood, resulting in a limited amount of allochthonous material and stable surface area for autochthonous production in open reaches.

As expected, we found a higher amount of chlorophyll *a* in open versus forested reaches, suggesting that light is limiting primary production in the forested reaches. We only found differences in biofilm biomass on rock substrates, emphasizing the importance of stable substrate for biofilm production in these streams. Differences in chlorophyll *a* and biofilm biomass potentially created an important difference in the trophic basis of production between reaches, which

we predicted to transfer to higher trophic levels. There were trends toward higher overall densities of benthic invertebrates in open reaches; however, benthic invertebrate densities also were more variable in open reaches. Contrary to our hypotheses, we did not observe any differences in the densities of scraping or shredding invertebrates between reaches. Because we only sampled invertebrates in one season (spring), we were unable to determine whether differences existed at other times of the year when food resources may differ more between open and forested reaches (e.g., during autumn leaf-fall for shredders). The lack of differences in functional feeding groups may also be due to invertebrate consumption by higher trophic levels. However, there were no consistent differences in the proportion of scraping insects (Ephemeroptera) in the guts of insectivorous fishes or salamanders. The only evident response of consumers to the shift in basal resources was the significantly higher densities of herbivorous fishes (*C. oligolepis*) in open reaches, presumably driven by higher amounts of algae.

Terrestrial invertebrates are also important food resources for some insectivorous fishes, and inputs were predicted to differ between paired reaches. Contradicting our expectations, we found higher densities of terrestrial invertebrate inputs in open reaches; however, similar results were also seen by Romaniszyn (2000) in Appalachian streams with cleared riparian zones. Higher densities in our study were primarily attributed to increased inputs of small-bodied Diptera and Collembola in open reaches. Correspondingly, there were trends toward larger animals and higher terrestrial invertebrate biomass in forested reaches. Because drift-eating fish are visual predators and tend to select larger invertebrates for consumption (Zaret 1980), these differences in terrestrial inputs were expected to translate into differences in fish diets. Water column fishes, especially cyprinids, showed trends of higher percent terrestrial prey in forested reaches, but our small sample sizes did not result in statistical significance. While some studies have found reduced dependence on terrestrial organic matter associated with riparian deforestation (Hicks 1997; Hession et al. 2002; England and Rosemond 2004), other results suggest that annual prey consumption by fishes can be similar even with drastically different inputs of terrestrial invertebrates (Kawaguchi and Nakano 2001). This may result from high fish mobility or invertebrate drift from upstream patches. Because stomach contents do not account for variable digestion of prey or the relative incorporation of terrestrial- versus aquatic-derived carbon in the fish tissue, we could not make any definitive conclusions about the relative contribution of food items to fish biomass.

Comparisons of fish size revealed inconsistent effects of riparian cover on population structure or sizes of individuals. For eight species, there were higher abundances of YOY individuals in the open reaches, possibly reflecting availability of shallow habitat in open reaches or behavioral avoidance of larger individuals in forested reaches. Two benthic invertivores (*N. leptacanthus* and *P. nigrofasciata*) were larger in forested reaches, suggesting possible differences in biomass of benthic invertebrates between reaches. Conversely, an invertivore, two generalist predators, and the herbivore *C. oligolepis* were larger in open reaches, potentially

reflecting higher nutritional quality and assimilation efficiency of algal-derived resources (Cummins 1974; Rosenfeld and Roff 1992). Food, habitat, and biotic interactions may all be important in explaining the distribution of adult and juvenile fishes.

### Comparison with similar research on urban riparian reforestation

This study used an exploratory approach comparing numerous variables between open and forested reaches to identify characteristics of stream reaches that may differ based on riparian canopy cover in urbanizing streams. Because we performed numerous paired *t* tests and regressions, there is a risk of type I error associated with a cutoff *p* value of 0.05 (Zar 1974). However, owing to the small sample size and powerful parametric statistical analyses performed, there is also a risk of type II error, such that there may be differences that are not detected at a significance level of  $p < 0.05$ . Thus, these results must be taken strictly as evidence of possible differences (or lack thereof) that provide predictions for further testing in urban streams.

Recent research by Hession et al. (2003) in the Piedmont of southeast Pennsylvania and northern Delaware provides an opportunity to evaluate the generality and significance of our results (see also Sweeney et al. 2004). The Hession et al. (2003) study included 12 pairs of sites with forested and nonforested (open) canopies that ranged in land cover from 1% to 91% urban (mean = 56.3% urban) and had similar criteria for site selection as our study. Where data were comparable, there were no conflicting results between the two studies (Table 5). Both indicated that open reaches had lower tree density, but trees in open reaches were larger in diameter. In addition, both studies showed that streams were narrower in open reaches, and there were no differences in depth between reaches. Lower amounts of large wood were found in open reaches in both studies, and Hession et al. (2003) demonstrated that bank stability was reduced in open reaches relative to forested reaches (not measured in this study). Other measures of physical habitat, including variability in velocity, depth, and particle size, were not different between reaches in either study, suggesting that reach-scale canopies do not control local habitat diversity. Both studies found higher chlorophyll *a* concentrations in open reaches; however, there were no clear differences in benthic invertebrates between reaches. In terms of fishes, both studies found significantly higher densities in open reaches, including higher densities of tolerant fish species. Although the studies measured trophic composition in different ways, both demonstrated a trophic response to increased algal resources in open reaches, as indicated by increased herbivore densities in this study and increased  $\delta^{13}\text{C}_{\text{periphyton}}$  in consumers in the Hession et al. (2003) study (Table 5). The consistent results in these two studies strengthen the conclusion that reach-scale riparian deforestation may result in trophic responses but has minimal effects on habitat quality and biotic integrity.

In this study, we primarily analyzed all biotic data in terms of relative abundances (unitless) and densities (i.e., per square metre of area) rather than per stream length because we felt that these were the most appropriate units for com-

**Table 5.** Responses to reach-scale riparian deforestation in Piedmont streams of southeastern Pennsylvania and northern Delaware ( $n = 12$  pairs) (Hession et al. 2003) and north-central Georgia ( $n = 5$  pairs) (this study).

Response variable	Hession et al.	This study	Response variable	Hession et al.	This study
Riparian vegetation			Organic matter		
Tree density	↓	↓	Leaf inputs	↓	nd
Tree size	↑	Trend ↑	Large wood	↓	↓
Litter quality	—	nd	Algae		
Channel morphology			Biofilm biomass	↑	Trend ↑
Width	↓	Trend ↓	Chlorophyll <i>a</i>	↑	↑
Depth	—	—	Diatom composition	—	nd
Bed slope	—	—	Benthic invertebrates <sup>a</sup>		
Physical habitat			Richness	nd	—
Rootwads	↓	nd	Density	nd	Trend ↑
Bank erosion rate	↑	nd	Terrestrial invertebrates		
Temperature	nd	Trend ↑	Density	nd	↑
Velocity variability	—	—	Biomass	nd	Trend ↓
Depth variability	—	—	Diversity	nd	↓
Particle size	—	—	Fishes		
Embeddedness	—	—	Density <sup>b</sup>	↑	↑
Nutrient concentrations			Biomass	↑	nd
SRP	↓	—	Tolerant	↑	↑
NH <sub>4</sub> -N	Trend ↓	—	Herbivores	nd	↑
NO <sub>2</sub> /NO <sub>3</sub> -N	—	↓	Trophic composition		
DIN:SRP	↑	—	δ <sup>13</sup> C <sub>periphyton</sub>	↑	nd
			% terrestrial in guts <sup>c</sup>	nd	Trend ↓

**Note:** An up arrow indicates significantly higher in open reaches ( $p < 0.05$ ), a down arrow indicates significantly lower in open reaches ( $p < 0.05$ ), trend indicates  $0.05 < p < 0.20$ , a dash indicates no difference ( $p > 0.20$ ), and nd indicates no data. SRP, soluble reactive phosphorus; DIN, dissolved inorganic nitrogen.

<sup>a</sup>Hession et al. (2003) used a dissimilarity index to compare benthic invertebrate composition between forested and nonforested reaches and found no difference.

<sup>b</sup>Sweeney et al. (2004) reported significantly higher densities of benthic invertebrates in forested reaches and no differences in fish densities between reaches when calculated per metre of stream length (versus per m<sup>2</sup> surface area).

<sup>c</sup>*Lepomis auritus* and *Cyprinella callistia*.

paring adjacent stream reaches. Given the reach conditions, we found higher densities of fishes, terrestrial invertebrate inputs, and algal chlorophyll *a* in open reaches, suggesting that this reach could support more primary producers and consumers on per square metre basis. However, because streams were ~20% wider in forested reaches compared with open reaches, there may be differences in overall production and nutrient uptake potential per metre of stream length (Sweeney et al. 2004).

### Implications for urban riparian reforestation

Although riparian buffers imply a goal of protecting stream ecosystems, local forested riparian areas are limited by their ability to mitigate upstream and downstream disturbances. Many studies have demonstrated the importance of catchment-scale land cover relative to local-scale land cover in driving habitat quality and biotic integrity (Richards et al. 1996; Roth et al. 1996; Allan et al. 1997). Although Roth et al. (1996) found that land cover within riparian areas was correlated with fish and habitat, these relationships only existed for riparian areas for the entire upstream network, not local riparian cover. This study directly tested changes associated with local riparian cover and also found that habitat quality and biotic integrity were not affected by local riparian deforestation. Although we were unable to test the rela-

tive importance of catchment-scale land cover (because of the small sample size of nested watersheds,  $n = 5$ ), these results suggest that preservation of forested riparian fragments is not adequate to protect stream ecosystems.

Our results demonstrate that reach-scale openings in riparian canopies can create local patches of increased food resources. Algal resources may be important for supporting food webs in urban systems where terrestrial organic inputs are minimized and altered storm hydrology affects organic matter retention. Although we observed trends of higher benthic invertebrate densities and significantly higher fish densities in open reaches, biomass and productivity may be similar between reaches, especially when calculated per linear length of stream reach (i.e., accounting for wider forested reaches). Further, the switch from allochthonous- to autochthonous-supported food webs at the reach scale, particularly in smaller headwater streams, may have important implications in terms of altered ecosystem function in these naturally forested landscapes (Cummins 1974).

We caution against concluding that forested canopies are not important, since the role of catchment land cover and extent and continuity of riparian forests were not tested in this study. These sites had >50% forest in the 30-m riparian zone in the upstream drainage network, so we do not know how these urbanizing streams would respond to a greater or more

complete loss of riparian cover and associated organic matter inputs. Other research shows that riparian cover in the upstream network is important for maintaining sensitive fishes, while local reductions in riparian forest cover increase species richness and abundance of tolerant fish (Roy 2004). Further studies addressing effects of local riparian forest cover with a range of network deforestation would be useful to understand the relative importance of upstream land cover in reach-scale stream conditions.

Previous studies have shown that over the long term, low levels of urbanization can negatively impact fish assemblages, structuring them toward more tolerant species that are habitat and trophic generalists (Weaver and Garman 1994; Wang et al. 2000; Walters et al. 2003). The maintenance of riparian forests has been successfully used to mediate the negative effects of agricultural and forestry practices on aquatic ecosystems; however, the relative benefits of riparian reforestation may be reduced in watersheds with increasing urbanization. In urban streams, alteration of stormwater hydrology (because of increases in impervious surfaces and number of stormwater pipes connected to streams) is thought to have an overarching influence on stream ecosystem integrity (Paul and Meyer 2001; Walsh 2004). Further, many urban streams are channelized and extensively piped (although not the case in these study streams), thus drastically altering stream habitat condition (Paul and Meyer 2001). Although we did not test the function of reach-scale riparian forests along a gradient of urbanization, our study suggests that at low levels of urbanization, reach-scale riparian forests provided minimal benefits to reach-scale stream condition. The combined results of this study and the Hession et al. (2003) study provide strong evidence that although riparian forest cover may be an important regulator of stream width, temperature, and the food/energy base at the reach scale, it does not dictate local stream habitat quality or biotic integrity. Thus, reach-scale riparian reforestation is necessary but not sufficient to protect aquatic resources in urbanizing landscapes. Watershed management, including stormwater management, is also needed to mitigate the impacts of urbanization.

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## **Appendix A**

Table A1 follows (pp. 2328–2329).

**Table A1.** List of all fish species collected in the study, their feeding guild, and their sensitivity categories.

Family and scientific name	Common name	Feeding guild	Sensitivity	All individuals		<i>t</i>	<i>p</i>		
				Open				Forest	
				<i>n</i>	Length (mm)			<i>n</i>	Length (mm)
<b>Petromyzontidae</b>									
<i>Ichthyomyzon gagei</i>	Southern brook lamprey	H		2	115	9	141	—	—
<b>Cyprinidae</b>									
<i>Camptostoma oligolepis</i>	Largescale stoneroller	H	C, T, G	1060	<b>59</b>	440	53	7.35	<0.001
<i>Cyprinella callistia</i> <sup>a</sup>	Alabama shiner	I	T, G	166	34	59	<b>55</b>	7.36	<0.001
<i>Cyprinella venusta</i> <sup>a</sup>	Blacktail shiner	I		47	24	22	<b>76</b>	14.04	<0.001
<i>Hybopsis</i> sp. cf. <i>winchelli</i>	Clear chub	BI		5	56	4	56	0.54	0.310
<i>Notropis longirostris</i>	Longnose shiner	I		107	26	8	33	1.69	0.065
<i>Notropis stilbius</i> <sup>a</sup>	Silverstripe shiner	I		107	28	17	<b>47</b>	5.24	<0.001
<i>Notropis xaenocephalus</i> <sup>a</sup>	Coosa shiner	I	E	257	42	230	<b>47</b>	4.86	<0.001
<i>Phenacobius catostomus</i>	Riffle minnow	BI	E	1	80	0	—	—	—
<i>Semotilus atromaculatus</i>	Creek chub	TG	C, T	43	87	54	86	0.11	0.458
<b>Catostomidae</b>									
<i>Hypentelium etowanum</i>	Alabama hog sucker	TG	T, G	210	83	194	81	0.72	0.236
<i>Moxostoma duquesnei</i>	Black redhorse	TG	C	52	<b>149</b>	18	113	3.00	0.002
<i>Moxostoma poecilurum</i>	Blacktail redhorse	TG	C	4	166	0	—	—	—
<b>Ictaluridae</b>									
<i>Ameiurus brunneus</i>	Snail bullhead	TG	C, G	1	145	1	56	—	—
<i>Ameiurus natalis</i>	Yellow bullhead	TG	C	1	127	0	—	—	—
<i>Noturus leptacanthus</i>	Speckled madtom	BI	C	69	42	17	<b>47</b>	1.87	0.036
<b>Fundulidae</b>									
<i>Fundulus stellifer</i> <sup>b</sup>	Southern studfish	TG		768	36	201	<b>54</b>	12.29	<0.001
<b>Poeciliidae</b>									
<i>Gambusia affinis</i>	Western mosquitofish	I	C, T	0	—	1	27	—	—
<b>Cottidae</b>									
<i>Cottus carolinae zopherus</i>	Coosa banded sculpin	BI	E	13	47	25	<b>52</b>	1.74	0.048
<b>Centrarchidae</b>									
<i>Lepomis auritus</i>	Redbreast sunfish	TG	C, T	169	62	168	<b>70</b>	2.93	0.002
<i>Lepomis cyanellus</i>	Green sunfish	TG	C, T	41	62	108	67	1.30	0.099
<i>Lepomis gulosus</i>	Warmouth	TG	C	0	—	1	80	—	—
<i>Lepomis macrochirus</i>	Bluegill	TG	C, T	251	<b>63</b>	365	58	4.04	<0.001
<i>Lepomis microlophus</i>	Redear sunfish	I	C	10	<b>68</b>	6	49	2.01	0.036
<i>Micropterus coosae</i>	Redeye bass	GC		10	78	14	96	1.27	0.108
<i>Micropterus punctulatus</i>	Spotted bass	GC	C	15	60	29	57	0.75	0.229
<i>Micropterus salmoides</i>	Largemouth bass	GC	C	19	96	15	69	1.49	0.073
<i>Pomoxis nigromaculatus</i>	Black crappie	TG	C	0	—	1	110	—	—
<b>Percidae</b>									
<i>Etheostoma scotti</i>	Cherokee darter	BI	E	157	42	128	41	0.49	0.313
<i>Etheostoma stigmaeum</i>	Speckled darter	BI	C	20	42	22	40	1.33	0.096
<i>Perca flavescens</i>	Yellow perch	TG	C, G	1	166	0	—	—	—
<i>Perca kathae</i>	Mobile logperch	BI		11	85	2	80	—	—
<i>Perca nigrofasciata</i>	Blackbanded darter	BI	C, T	99	48	63	<b>59</b>	4.36	<0.001

**Note:** Comparison of mean fish standard lengths between open and forested reaches (two-sample *t* test assuming unequal variances) for all individuals I, invertivore; BI benthic invertivore; TG, trophic generalist; GC, generalized carnivore. Sensitivity categories: E, endemic; C, cosmopolitan; T, tolerant; (*p* < 0.05). Species with less than four individuals in one or both reaches were not analyzed (indicated by a dash). *n* is the number of individuals.

<sup>a</sup>Difference in length because of YOY fishes in the open reach of Weatbrook Creek.

<sup>b</sup>Difference in length because of YOY fishes in the open reaches of multiple streams.

YOY excluded					
Open		Forest		<i>t</i>	<i>p</i>
<i>n</i>	Length (mm)	<i>n</i>	Length (mm)		
2	115	9	141	—	—
755	65	147	<b>71</b>	4.46	<0.001
34	61	40	<b>66</b>	1.98	0.026
3	66	21	78	—	—
5	56	4	56	0.535	0.310
11	51	3	46	—	—
9	61	13	54	1.44	0.090
109	52	173	52	0.42	0.338
1	80	0	—	—	—
30	104	41	99	0.9	0.187
88	<b>120</b>	97	109	3.33	<0.001
39	<b>175</b>	11	140	4.45	<0.001
4	166	0	—	—	—
1	145	1	56	—	—
1	127	0	—	—	—
62	44	15	<b>49</b>	2.59	0.007
138	69	120	68	1.07	0.142
0	—	1	27	—	—
5	55	19	55	0.04	0.484
112	75	144	75	0.18	0.429
35	65	97	69	1.09	0.141
0	—	1	80	—	—
221	<b>67</b>	285	63	3.23	<0.001
9	<b>71</b>	5	50	2.01	0.040
6	99	10	115	1.41	0.093
0	—	1	126	0.749	0.229
7	164	4	118	1.37	0.102
0	—	1	110	—	—
157	42	125	42	0.125	0.450
17	<b>45</b>	21	40	3.22	0.001
1	166	0	—	—	—
11	85	2	80	—	—
72	55	56	<b>62</b>	2.98	0.002

and with YOY individuals excluded. Feeding guilds: H, herbivore; G, habitat generalist. Bold numbers indicate significantly longer lengths.