

## Comparison of insect communities between adjacent headwater and main-stem streams in urban and rural watersheds

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**Abstract.** Watershed urbanization decreases diversity and taxonomic richness of aquatic insect communities, and headwater streams are particularly susceptible to degradation from urbanization. Patterns of taxon loss between urban headwater communities and communities in adjacent downstream, higher-order reaches might indicate which processes are controlling taxon loss and the extent to which unique headwater taxa are lost after urbanization. We compared insect communities in urban and rural watersheds and investigated if community similarity between headwater streams and adjacent higher-order main-stem reaches was greater in urban than in rural watersheds. We sampled insect communities in 3 urban and 3 rural watersheds in Maryland's Piedmont region during 3 seasons. Mean taxonomic richness was 4.3× greater and the Shannon diversity index was 1.8× greater in rural than in urban headwater streams. Simpson's index was 1.9× greater in urban than in rural headwater streams. The Jaccard similarity index calculated between headwater and main-stem communities was 1.6× greater for urban sites than rural sites during autumn, and the proportion of headwater taxa shared with the main-stem community was 1.8× greater for urban than rural sites. Redundancy analysis also indicated significantly greater similarity between urban headwater and main-stem communities than between rural headwater and main-stem communities. As expected, urbanization decreased diversity, and the communities remaining in urban headwaters were mostly subsets of the communities in the main-stem streams. This result suggested that taxa unique to headwaters were at the greatest risk of local extirpation after watershed urbanization. A significant interactive effect of landuse type and the longitudinal position of a reach along the headwater on taxonomic richness and the Jaccard index suggested that patterns of taxon loss partially depended on the proximity of a headwater reach to the main-stem stream. Overall, the results suggested that water- and habitat-quality degradation were not the only effects of watershed urbanization that determined the composition of insect communities in urban headwaters.

**Key words:** aquatic insects, watershed urbanization, headwater streams, community similarity, richness, diversity, redundancy analysis, longitudinal patterns.

Watershed urbanization and other anthropogenic landuse changes are causing losses of native aquatic insect species from lotic ecosystems (Paul and Meyer 2001, Walsh et al. 2001, McKinney 2002, Moore and Palmer 2005). Human activities in the watershed impair stream water and habitat quality, which, in turn, cause local extirpations of intolerant taxa, decreased community richness, and increased dominance of tolerant taxa (Walsh et al. 2005). However, degradation of stream water and habitat quality are not the only effects of watershed urbanization that potentially decrease stream insect diversity. Impacts to

the terrestrial environment and landscape-scale changes to the stream network often are ignored but also might determine species richness of insect communities in urban streams (Vinson and Hawkins 1998). The composition of insect communities in surrounding streams (Sanderson et al. 2005), the dispersal capabilities of adult aquatic insects (Palmer et al. 1996, Hoffsten 2004, Petersen et al. 2004), and dispersal constraints at local (Blakely et al. 2006) and watershed scales (Bond and Lake 2003) all have been proposed as important factors affecting insect community composition in streams draining urbanized watersheds. Properties of stream networks, such as drainage density and the arrangement of streams in the network, also might influence how urbanization

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affects insect communities (Meyer and Wallace 2001, Grant et al. 2007). Therefore, examination of the effects of watershed urbanization on aquatic insects by comparing communities in adjacent streams might indicate whether: 1) processes other than habitat and water-quality degradation decrease diversity and 2) taxa unique to specific habitats are being lost.

The effects of watershed urbanization are particularly important for aquatic insect communities in the headwaters of stream networks. Headwater streams make up an estimated 70 to 75% of the stream channel length in the USA, affect the health of the entire stream network, and are unique environments that often contain rare species (Leopold et al. 1964, Meyer and Wallace 2001, Gomi et al. 2002, Meyer et al. 2003, 2007, Lowe and Likens 2005). They often are absent from maps and surveys and frequently are excluded from conservation and mitigation programs, despite their importance and their status as the lotic ecosystems most threatened by anthropogenic activities (Leopold et al. 1964, Meyer and Wallace 2001, Gomi et al. 2002, Meyer et al. 2003, 2007). Moreover, their small size and inconspicuous nature can increase the occurrence and severity of effects of urbanization (Meyer and Wallace 2001), such as increased impervious surfaces, toxic chemical inputs, and riparian deforestation, that can degrade water and habitat quality in headwater streams (Sweeney 1993, Gomi et al. 2002, Gage et al. 2004). In addition to experiencing degradation, headwater streams in urbanized watersheds sometimes are converted to drainage systems and destroyed altogether (Meyer and Wallace 2001).

The type and quality of habitats at various spatial scales determine local species composition in streams by filtering from the regional species pool those species whose habitat requirements are not met (Poff 1997, Malmqvist 2002, Lamouroux et al. 2004). Habitats differ between headwaters and downstream reaches in watersheds unaffected by urbanization, and taxonomic composition of communities in headwater and downstream reaches is expected to differ (Meyer and Wallace 2001, Meyer et al. 2007). In urban streams, poor habitat might decrease taxonomic richness by filtering species that normally would be present in an unimpacted stream from the regional pool. If the filtering effect of habitat degradation caused by urbanization is similar in headwaters and downstream reaches, then the same group of tolerant taxa might persist in both locations. If dispersing adults are less frequent in urban watersheds, then the regional species pool might shrink, thereby intensifying the effects of water- and habitat-quality degradation on insect diversity (Heino et al. 2003, Petersen et al. 2004). Specifically, restricted adult movement, low adult

survival, and habitat fragmentation in urban watersheds might limit the regional species pool at headwaters to only those taxa found in downstream reaches (Smith 2006). The absence of unique headwater taxa from the regional species pool might cause communities in affected urban headwaters and healthy downstream reaches to become similar.

The river continuum concept predicts a shift from taxa that use allochthonous food sources in headwater communities to taxa that use autochthonous food sources in mid-order streams (Vannote et al. 1980). Riparian deforestation associated with urbanization can decrease allochthonous inputs and organic matter retentiveness along the entire stream network (Paul and Meyer 2001). Decreased allochthonous food resources and increased light penetration can shift the trophic structure of urban headwater insect communities to a form expected in open-canopied mid-order reaches with abundant autochthonous food resources (Sweeney 1993, Delong and Brusven 1998, Meyer and Wallace 2001). This shift in trophic structure could result in greater than expected similarity between communities in headwater and higher-order reaches in urbanized watersheds even if taxonomic richness does not decline.

We examined insect community composition in headwater and downstream reaches in urban and rural watersheds. The objective of our study was to characterize patterns of taxon loss from headwater streams in urbanized watersheds. We reasoned that patterns of taxon loss from headwater streams might indicate mechanisms (in addition to water- and habitat-quality degradation) that decrease diversity (Blakely and Harding 2005) and might show specific ways in which unique headwater taxa respond to urbanization. We used 3 kinds of comparisons to discriminate among mechanisms of taxon loss in urbanized streams. First, we compared insect communities in headwaters of urban watersheds to insect communities in headwaters of rural watersheds. We expected to find lower diversity in urban than in rural headwaters. Second, we compared the similarity of insect communities in headwaters to communities in their adjacent main-stem reaches between sites with urban and rural headwaters. We hypothesized that insect communities in headwater streams and adjacent main-stem reaches would be more similar and that a larger proportion of taxa would be shared between headwater and main-stem reaches within sites with urban headwaters than sites with rural headwaters. Third, we compared similarity of insect communities in 3 different reaches along headwater streams to communities in their adjacent main-stem reach of the same stream between sites with urban and rural

TABLE 1. Watershed landuse statistics for each headwater stream and associated main-stem reach at the 6 study sites. Headwater watersheds include all area that drained to the mouth of the headwater stream. Main-stem watersheds included all area that drained to the downstream portion of the sample reach.

Landuse type	Site	Headwater stream			Main-stem stream				
		Watershed area (km <sup>2</sup> )	% urban	% agriculture	% forest	Watershed area (km <sup>2</sup> )	% urban	% agriculture	% forest
Rural	R-DRK	1.3	12.8	28.4	58.9	30.6	10.7	36.6	52.8
	R-MPE	0.13	0.0	0.0	100.0	98.7	35.1	40.4	24.4
	R-SNC	2.3	1.7	82.6 <sup>a</sup>	15.7	162.1	49.9	20.8	29.3
Urban	U-RBR	3.4	88.6	1.2	10.2	9.1	39.1 <sup>b</sup>	35.3	25.6
	U-SAL	1.0	84.1	0.0	15.9	31.6	72.6	5.1	22.2
	U-SPD	0.78	98.9	0.0	1.1	7.0	98.2	0.0	1.8

<sup>a</sup> Agricultural area is overestimated because some land is being replanted with deciduous trees and all agriculture occurs within a state park

<sup>b</sup> Urban area is underestimated because of new construction not in GISHydro2000 (2<sup>nd</sup> edition; Department of Civil and Environmental Engineering, College Park, Maryland, and the Maryland State Highway Administration, Baltimore, Maryland)

headwaters. We hypothesized that longitudinal patterns of similarity between individual headwater reaches and the main stem would differ between sites with urban and rural headwaters.

## Methods

### Site selection and classification

Three urban and 3 rural study sites were chosen from the Piedmont region of Montgomery and Howard counties, Maryland (Table 1, Fig. 1). A study site consisted of a headwater stream and the reach of the higher-order main-stem stream at the confluence of the headwater and the main-stem stream (adjacent main-stem reach; Fig. 1). Sampling was done in reaches near the mouth, near the source, and midway along each headwater and at the top and bottom of the main-stem reach (Fig. 1) for a total of 5 sampling locations at each site (30 sampling locations across 6 sites). Headwater streams were perennial and had no perennial tributaries. One urban headwater stream had an intermittent tributary. Adjacent main-stem reaches were all part of 2<sup>nd</sup>- or higher-order streams. Stream order for main-stem reaches was determined using US Geological Survey 1:24,000-scale quadrangles (revised, photo-revised, or photo-inspected between 1973 and 1993). Land use associated with the entire watershed upstream from the mouth of each headwater stream was determined from Maryland Department of Planning geographical information system (GIS) land coverages (30-m resolution) available in the ArcView (version 3.3; Environmental Systems Research Institute, Redlands, California) supplement program GISHydro2000 (2<sup>nd</sup> edition; Department of Civil and Environmental Engineering, College Park, Maryland; Moglen 2005). Study sites and

headwater streams were defined as *urban* if land use in the watershed of the headwater streams was  $\geq 75\%$  commercial or residential or *rural* if land use in the watershed was  $\geq 75\%$  agricultural or forested.

Headwater streams were visited in random order and were sampled during base flow conditions. Conductivity and pH were measured using a YSI model 556 multiprobe (Yellow Springs Instruments, Yellow Springs, Ohio) during summer 2004 at 1 riffle in each of the 3 reaches along each headwater stream (Fig. 1). Physical characteristics were measured in the same reaches during summer 2006. Ten transects spaced 2 m apart were set out along a 20-m reach centered at the middle of each riffle sampled in 2004. The reach included the riffle, and run and pool habitat. Percentage of slope between the ends of the reach was measured using a clinometer. Stream width, thalweg depth, and the dominant substrate type were measured at each transect. The substrate type that made up  $>50\%$  of a 1-m<sup>2</sup> area of the stream bottom was designated the dominant substrate type at each transect. Riparian canopy cover was measured from digital photos of the canopy directly above the middle of each reach. The open area in each photo was analyzed with ImageJ (National Institutes of Health, Washington, DC). Discharge was determined at the most downstream reach in each headwater stream from stream cross-sectional area and stream flow measured with a Marsh–McBirney Flow-Mate model 2000 flow meter (Marsh–McBirney, Frederick, Maryland). Differences in mean discharge, mean slope, mean width, mean depth, mean percentage of canopy cover, conductivity, and pH between urban and rural headwater streams were tested using 1-tailed Wilcoxon rank sum tests because of a priori expectations about the distributions of values of chemical and

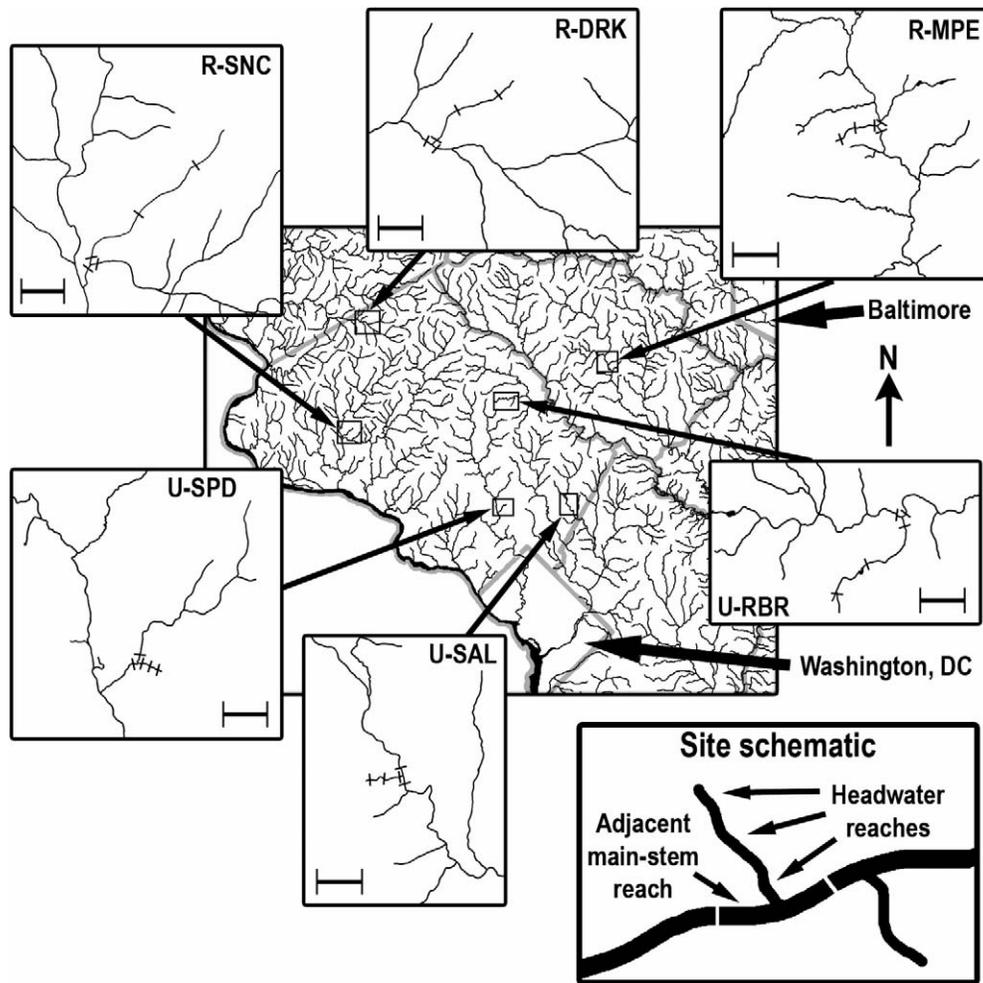


FIG. 1. Study sites in Montgomery and Howard counties, Maryland. The site schematic on the bottom right shows a generalized view of the sampling locations within a site. Sites consisted of a headwater stream and its adjacent main-stem reach. The adjacent main-stem reach is the reach on the higher-order stream into which the headwater flows and is located at the confluence of the headwater with the main-stem stream (delineated by white lines on the main-stem stream). Three reaches (upstream, midstream, downstream) were sampled in each headwater. Each small map shows the details of a sampling site (small lines indicate the center of sample reaches), and the arrows point to the locations of the sites. Scale bars on each site map are 0.25 km. Site codes beginning with R are rural; codes beginning with U are urban.

physical characteristics of urban and rural headwaters (Hollander and Wolfe 1973).

#### *Insect sampling and processing*

Benthic communities were sampled in riffles in the headwater streams and in main-stem reaches during spring (May–June), summer (July–August), and autumn (September–October) 2004. Sites were visited in random order during base flow. Only riffles were sampled because this habitat usually contains highly diverse communities of aquatic insects that respond to urbanization, can be sampled quantitatively, and are comparable between streams (Karr 1999, Roy et al. 2003). In each headwater stream, one sample was

collected from a randomly selected location in each of the 3 riffles where water chemistry was measured. Samples were taken with a 0.04-m<sup>2</sup> Surber sampler (mesh size = 250 μm) to a depth of 8 to 10 cm. In each main-stem reach, one sample was collected from a randomly selected location in the first riffle upstream and in the first riffle downstream of the confluence with the headwater stream. Samples were preserved in 100% ethanol (final concentration ≥80%). In the laboratory, the entire sample was sorted under magnification with a dissecting microscope. All aquatic insects except Chironomidae were removed from the sample debris and identified to the lowest practical taxonomic level (genus or species in most cases) using

local and regional keys. Chironomidae were excluded from the analyses.

#### *Data analysis*

*Composite samples.*—Artificial composite samples representing each headwater stream in each season were created by combining data from the 3 riffle samples within each headwater stream and season. Artificial composite samples representing each main-stem reach in each season were created by combining data from samples from the upstream and downstream riffles within each main-stem reach and season. Composite samples were used when comparing diversity measurements between headwaters, when comparing similarity measures between sites, and for the redundancy analysis (RDA). Uncomposited individual reach samples for the headwaters were used when examining longitudinal patterns along headwaters.

*Community composition in headwater streams.*—Diversity was quantified by mean number of taxa ( $S$ ), the mean Shannon diversity index ( $H'$ ), and the mean Simpson's index ( $D$ ) (Magurran 1988). Values for  $H'$  usually fall between 1.5 (low diversity) and 3.5 (high diversity) and rarely are  $>4.5$ . The range of values for  $D$  depends on the underlying distribution of the population, and low values represent high evenness (Magurran 1988). The mean relative densities of functional feeding groups (% predators, % filterers, % collector-gatherers, % scrapers, and % shredders) also were calculated for each headwater stream. Taxa were assigned to functional feeding groups on the basis of Barbour et al. (1999) and Merritt and Cummins (1996).  $D$  values were  $\log_{10}(x)$ -transformed and % predators, % scrapers, and % shredders were  $\arcsin(\sqrt{x})$ -transformed to meet the assumption of homogeneity of variance.  $S$ ,  $H'$ ,  $D$ , % predators, % filterers, % collector-gatherers, % scrapers, and % shredders were compared between urban and rural headwater streams in 3 seasons with a repeated-measures analysis of variance (ANOVA) (Proc Mixed; SAS, version 9.1; SAS Institute, Cary, North Carolina). A separate ANOVA was done for each functional feeding group.

*Community similarity between headwater streams and main-stem reaches.*—Community similarity was quantified with the Jaccard index ( $C_j$ ) (Magurran 1988), the Morisita–Horn index ( $C_{mH}$ ) (Magurran 1988), and the mean proportion of headwater taxa shared with their respective main-stem community ( $C_p$ ).  $C_j$  and  $C_p$  measure similarity on the basis of taxon presence/absence and  $C_{mH}$  measures similarity on the basis of densities of each taxon. Each similarity index ranges between 0 (no taxa in common) and 1 (identical

communities).  $C_j$  and  $C_{mH}$  were both used because  $C_{mH}$  is considered a better measure of overall community similarity than  $C_j$  (Magurran 1988), but the focus of our study also included taxonomic similarities, which is best measured by  $C_j$ .  $C_p$  is a contrived index that measures the proportion of taxa in the headwater that also are found in the adjacent main-stem reach. This index measures a different form of similarity from  $C_j$ . The similarity indices were calculated between the composited headwater and main-stem communities for each site and season. Each index was compared between urban and rural sites for 3 seasons with a repeated-measures ANOVA (Proc Mixed). All assumptions of ANOVA were met. ANOVA showed a significant interaction effect of land use and season on  $C_j$ . Therefore, post-hoc examinations of treatment means for each season were done with a Tukey–Kramer adjustment instead of examining treatment main effects (Sokal and Rohlf 1981).

*RDA.*—RDA was used to further characterize similarities between headwater stream and main-stem reach communities from rural and urban sites. RDA is a constrained form of principle component analysis (Leps and Šmilauer 2003) and relates the underlying structure of community data sets to explanatory variables. In this case, the explanatory variable was the stream/reach type (i.e., urban headwater stream, rural headwater stream, urban main-stem reach, and rural main-stem reach). Nine composite samples (3 sites  $\times$  3 seasons) were used for each stream/reach type. All analyses were done with CANOCO for Windows (version 4.5; Biometris—Plant Research International, Wageningen, The Netherlands). A linear response model (RDA) was selected on the basis of the results of a detrended correspondence analysis (CANOCO). Season was used as a covariable in all analyses. First, all 9 samples for each of the 4 stream/reach types were analyzed together. A Monte Carlo permutation test was used to determine if stream/reach type explained a significant amount of the variation among insect communities. Resampling was restricted to within each season, and 1000 permutations were run. RDA also was done with pairs of stream/reach types: 1) urban headwater and rural headwater, 2) urban main-stem and rural main-stem, 3) urban headwater and urban main-stem, and 4) rural headwater and rural main-stem. A Monte Carlo test was used to determine if stream/reach type explained a significant amount of the variation among insect communities in each pairwise data set. Resampling was restricted to within each season, and 1000 permutations were run for each pairwise analysis.

*Longitudinal patterns in headwater streams.*—Longitudinal patterns of diversity and similarity were tested

TABLE 2. Physical and chemical characteristics of headwater streams. The dominant substrate in a reach made up >50% of the stream bottom in a 1-m<sup>2</sup> area in the middle of the stream at 10 transects from 3 reaches. Possible substrates include fine silt, sand (<2 mm and granular), gravel (2–10 mm), pebble (1–6.4 cm), cobble (6.4–25.6 cm), boulder (>25.6 cm), and bedrock. Wilcoxon rank sum tests were used to compare characteristics between rural and urban sites. NS = not significant.

Stream type	Stream pair	Base flow discharge (m <sup>3</sup> /s)	Slope <sup>a</sup> (%)	Width <sup>b</sup> (m)	Depth <sup>b</sup> (cm)	Dominant substrate	Canopy cover <sup>a</sup> (%)	Conductivity <sup>a</sup> (mS/cm)	pH <sup>a</sup>
Rural	R-DRK	0.0071	1.2	1.8	7.0	Gravel	84.4	0.12	7.1
	R-MPE	0.0029	3.7	0.6	3.8	Sand	84.9	0.04	6.8
	R-SNC	0.0271	2.3	2.5	11.7	Cobble	82.7	0.22	7.2
Urban	U-RBR	0.0182	0.5	2.5	19.6	Cobble	55.6	0.16	7.1
	U-SAL	0.0096	3.2	3.0	18.0	Cobble	63.4	0.42	7.2
	U-SPD	0.0086	1.3	3.0	21.1	Cobble	79.0	0.27	6.9
Wilcoxon rank sum test		NS	NS	NS	<i>p</i> = 0.05	NA	<i>p</i> = 0.05	NS	NS

<sup>a</sup> Mean of 3 reaches

<sup>b</sup> Mean of 10 measures at 3 reaches

for a significant interaction between landuse type and position (upper, middle, lower) of a reach along the headwater stream. *S* was calculated for each headwater reach and season and was compared among land-use types, positions, and seasons with a repeated-measures ANOVA (Proc Mixed). *C<sub>j</sub>* and *C<sub>mH</sub>* were calculated between the communities from individual headwater reaches and their adjacent main-stem reach (composite) for each season and were compared among land-use types, positions, and seasons with a repeated-measures ANOVA (Proc Mixed). The data were analyzed as a split-split-plot design in space and time using the REPEATED option of SAS to account for repeated measures from each season. *S* values for individual reaches along the headwater and *C<sub>j</sub>* and *C<sub>mH</sub>* values calculated between individual headwater reaches and the composited main-stem communities were subplots within urban and rural site whole plots. Mean *S* was log<sub>10</sub>(*x* + 1)-transformed to satisfy the assumption of homogeneity of variance. Individual reach means were compared with a Tukey–Kramer adjustment.

**Results**

*Characteristics of watersheds and headwater streams*

By design, forested and agricultural land uses were predominant in the watersheds of rural headwater streams, and urban land use was predominant in the watersheds of urban headwater streams (Table 1). Headwater watersheds ranged in size from 0.13 km<sup>2</sup> to 3.4 km<sup>2</sup> (Table 1). The largest headwater watershed (U-RBR) was urban, and the next 2 largest (R-SNC, R-DRK) were rural. The smallest headwater watershed (R-MPE) was rural. Main-stem watersheds ranged in size from 7.0 km<sup>2</sup> to 162.1 km<sup>2</sup>. The 2 largest main-stem watersheds (R-SNC and R-MPE) were rural and the 2 smallest (U-SPD and U-RBR) were urban.

Urban headwater streams were deeper than rural headwater streams (Wilcoxon rank sum test, *p* = 0.05; Table 2), and % canopy cover was greater for rural headwater streams than urban headwater streams (Wilcoxon rank sum test, *p* = 0.05; Table 2). Only 1 riffle at an urban headwater stream had no canopy cover, but the riparian zone at that riffle was forested a few meters from the stream bank. Cobble substrate was the most commonly measured benthic substrate in urban headwater streams, whereas gravel, sand, and cobble were the most common substrates in rural headwater streams (Table 2).

*Insect communities*

One hundred one taxa of aquatic insects from 9 orders were collected during the study (see Smith 2006 for a complete list of taxa). Total Ephemeroptera, Plecoptera, and Trichoptera taxa collected from a single season and site ranged from 7 to 17 taxa for rural main-stem reaches, 4 to 15 taxa for urban main-stem reaches, 13 to 19 for rural headwater streams, and 1 to 6 for urban headwater streams. *Baetis* (Ephemeroptera:Baetidae), *Hydropsyche* (Trichoptera:Hydropsychidae), and *Cheumatopsyche* (Trichoptera:Hydropsychidae) were abundant at all sites. *Leuctra* (Plecoptera:Leuctridae) and *Diplectrona modesta* (Trichoptera:Hydropsychidae) were abundant in rural headwater streams. *Stenelmis* (Coleoptera:Elmidae) was occasionally abundant in both rural and urban sites. The most taxa and greatest densities of Plecoptera usually were found in rural headwater streams.

*Community composition in headwater streams*

*S* (*F*<sub>1,4</sub> = 20.85, *p* = 0.01; Fig. 2A) and *H'* (*F*<sub>1,6.35</sub> = 45.68; *p* = 0.0004; Fig. 2B) were significantly lower and mean *D* (*F*<sub>1,5.14</sub> = 18.92, *p* = 0.007; Fig. 2C) was significantly greater in urban than rural headwater

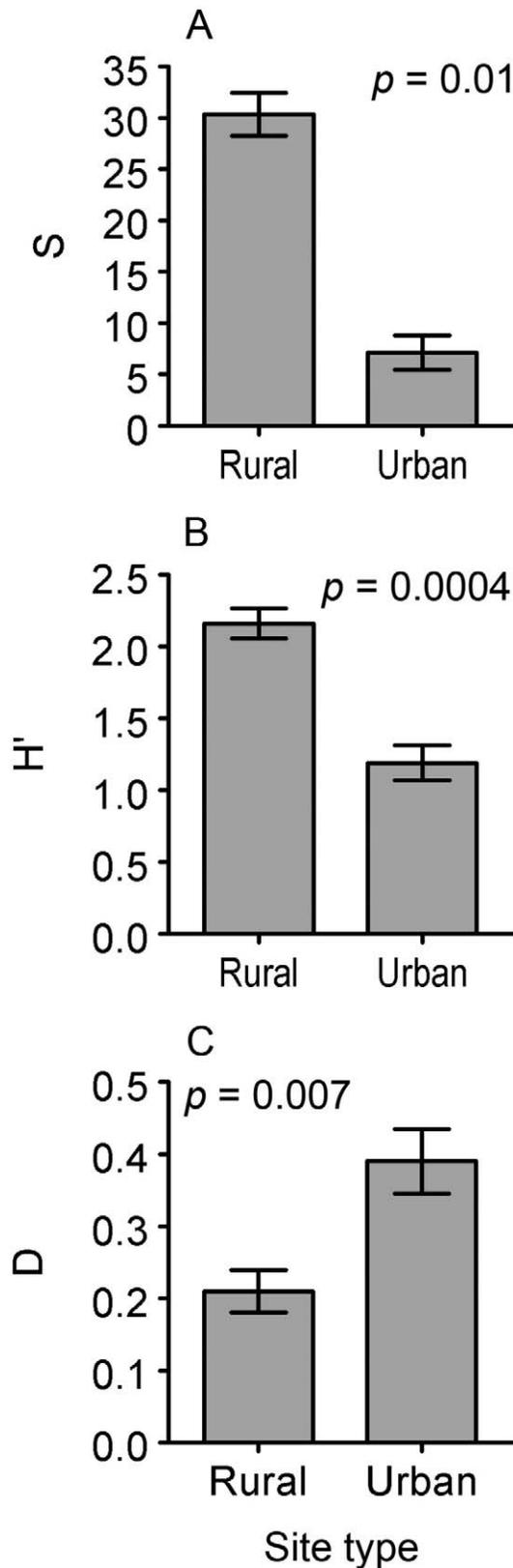


FIG. 2. Mean ( $\pm 1$  SE) taxonomic richness (S) (A), Shannon diversity index ( $H'$ ) (B), and Simpson's diversity index (D) (C) for rural and urban headwater streams.

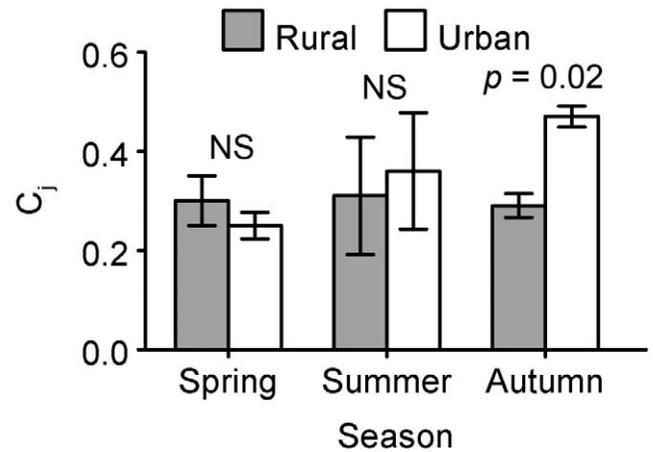


FIG. 3. Mean ( $\pm 1$  SE) Jaccard index ( $C_j$ ) for each season for urban vs rural sites. NS = rural and urban sites not significantly different within a season.

streams. The values indicated that taxonomic diversity of headwater communities was greater at rural than at urban sites.

Percent predators ( $F_{1,4} = 11.43, p = 0.03$ ) was significantly lower in urban (0.38%) than in rural (14.4%) headwater streams. Percent filterers ( $F_{1,4} = 5.04, p = 0.08$ ), % collector/gatherers ( $F_{1,4} = 0.10, p = 0.77$ ), % scrapers ( $F_{1,4} = 2.12, p = 0.22$ ), and % shredders ( $F_{1,4} = 1.61, p = 0.27$ ) did not differ between urban and rural headwater streams. Percent filterers was highly variable, but tended to be higher than % collector/gatherers, % scrapers, and % shredders in both urban (69.3%) and rural (36.6%) headwater streams.

*Community similarity between headwater streams and main-stem reaches*

$C_j$ , which measured similarity between headwater and main-stem communities on the basis of taxon presence/absence, was significantly influenced by the interaction between land-use type and season ( $F_{2,4.17} = 13.18, p = 0.02$ ).  $C_j$  did not differ between rural and urban sites in spring (Tukey-Kramer,  $p = 0.95$ ) or summer (Tukey-Kramer,  $p = 1.00$ ), but was significantly greater in urban than in rural sites in autumn (Tukey-Kramer,  $p = 0.02$ ) (Fig. 3).  $C_{mH}$ , which measured similarity between headwater and main-stem communities on the basis of taxonomic composition and densities, did not differ between rural and urban sites ( $F_{1,4} = 0.74, p = 0.44$ ).  $C_{mH}$  values were highly variable for both rural (0.95–0.01) and urban (0.96–0.05) sites.

$C_p$  was significantly greater for urban than rural sites ( $F_{1,4} = 9.58, p = 0.04$ ; Fig. 4). Thus, a greater proportion of taxa in headwater communities also

were found in the adjacent main-stem community in urban than in rural sites. The number of taxa found in the headwater stream but not in the main-stem reach ranged from 19 to 34 in rural sites and from 1 to 4 in urban sites (Table 3). The unique headwater taxa in rural headwater streams belonged to 8 orders including many Ephemeroptera, Plecoptera, and Trichoptera taxa (Table 3). The unique headwater taxa in urban headwater streams belonged only to Odonata and Diptera. Four of the 6 unique urban headwater taxa, including *Ischnura* (Odonata:Coenagrionidae), *Calopteryx maculata* (Odonata:Calopterygidae), *Aedes* (Diptera:Culicidae), and *Odontomyia* (Diptera:Stratiomyidae), were not part of any rural headwater community.

#### RDA

Stream/reach type explained 24.3% of the total variance of insect taxonomic composition in the RDA that included samples from all 4 stream/reach types (Fig. 5). Season explained only 6.4% of the total variance. The 1<sup>st</sup> axis explained 89.5% of the total residual variance explained by stream/reach type, and the 2<sup>nd</sup> axis explained 13.6% of the total residual variance explained by stream/reach type (total of 94.2% of the variance explained by stream/reach type). The communities in rural headwater streams were separated from communities in the other 3 stream/reach types along the 1<sup>st</sup> axis. Urban headwater and main-stem and rural main-stem communities were separated along the 2<sup>nd</sup> axis. The absence of taxon vectors in the direction of the urban headwater reaches occurred because insect densities were very low in urban headwater reaches. The Monte Carlo permutation test for the analysis using all 4 stream/reach types detected a significant effect of stream/reach type on insect community composition ( $F = 3.50$ ,  $p = 0.001$ ). The Monte Carlo permutation tests for the pairwise RDAs also found a significant effect of stream/reach type when rural headwater and rural main-stem communities ( $F = 4.10$ ,  $p = 0.003$ ) and rural headwater and urban headwater communities ( $F = 4.70$ ,  $p = 0.002$ ) were compared. No effect of stream/reach type was found when urban headwater and urban main-stem communities ( $F = 1.52$ ,  $p = 0.16$ ) and rural main-stem and urban main-stem communities ( $F = 1.55$ ,  $p = 0.14$ ) were compared.

#### Longitudinal patterns in headwater streams

Landuse type affected longitudinal patterns of  $S$  along headwater streams (land use  $\times$  reach position interaction,  $F_{2,9} = 8.7$ ,  $p = 0.008$ ; Fig. 6A).  $S$  was greater at upstream and downstream rural reaches than at

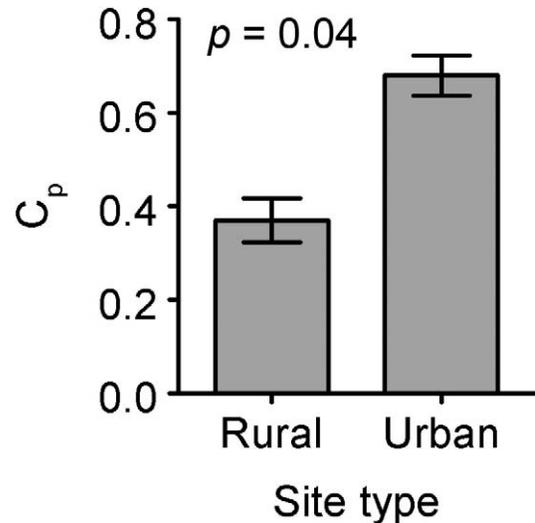


FIG. 4. Mean ( $\pm 1$  SE) proportions of headwater taxa shared with the main-stem community ( $C_p$ ) sampled for urban vs rural sites.

upstream (Tukey–Kramer adjustment,  $p = 0.009$  and  $p = 0.01$ , respectively) and midstream (Tukey–Kramer adjustment,  $p = 0.03$  and  $p = 0.05$ , respectively) urban reaches, and  $S$  was greater at midstream rural reaches than at upstream (Tukey–Kramer adjustment,  $p = 0.02$ ) urban reaches (Fig. 6A).  $S$  was lower at upstream urban reaches than at downstream urban reaches (Tukey–Kramer adjustment,  $p = 0.007$ ).  $S$  did not differ among reaches within rural sites (Fig. 6A).

Landuse type affected longitudinal patterns of  $C_j$  along headwater streams ( $F_{2, 31.1} = 3.63$ ,  $p = 0.038$ ; Fig. 6B), but did not affect longitudinal patterns of  $C_{mH}$  ( $F_{2,8,54} = 1.61$ ,  $p = 0.25$ ).  $C_j$  was greater for downstream reaches than for midstream (Tukey–Kramer adjustment,  $p = 0.04$ ) and upstream (Tukey–Kramer adjustment,  $p = 0.0002$ ) reaches in urban sites (Fig. 6B).  $C_j$  did not differ among reaches within rural sites.  $C_{mH}$  values were extremely variable.

## Discussion

### Patterns of taxonomic diversity and similarity

As expected from previous studies (Paul and Meyer 2001, Walsh et al. 2001, Moore and Palmer 2005), insect communities were less diverse in urban than in rural headwater streams (Fig. 2). In our study, % predators was significantly lower in urban than in rural headwater streams, a result that also indicated negative effects of human activities on the urban headwater streams (Kerans and Karr 1994). Semi-voltine insect predators often are absent from streams draining urbanized watersheds (DeWalt et al. 2005).

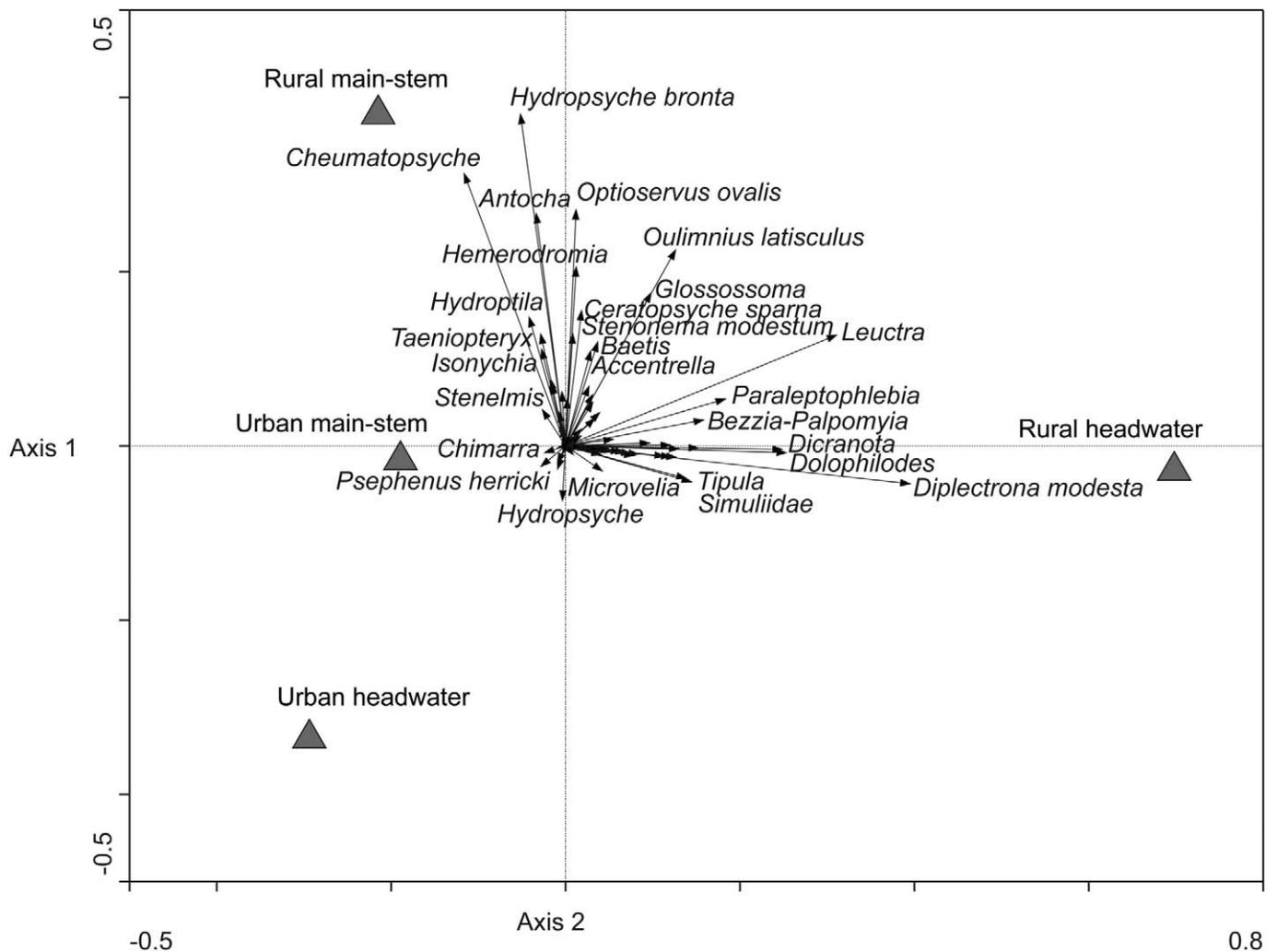


FIG. 5. Biplot resulting from redundancy analysis including all 4 stream/reach types (urban and rural headwater and urban and rural main stem). Taxa are represented by vectors, and stream/reach types are represented as centroids (triangles). The distance between centroids represents the difference in the community composition of the stream/reach types. The length of the vector represents the amount of variance in community composition explained by that taxon. Only the longest vectors in each quadrant were labeled to simplify presentation. The 1<sup>st</sup> axis explained 89.5% of the total residual variance explained by stream/reach type and the 2<sup>nd</sup> axis explained 13.6% of the total residual variance explained by stream/reach type (total of 94.2% of the variance).

The measures of community similarity that were based on taxon presence/absence ( $C_j$  [Fig. 3] and  $C_p$  [Fig. 4]) did differ significantly between rural and urban sites and indicated greater similarity between headwater and main-stem communities in urban than in rural watersheds.  $C_{mH}$  did not differ between urban and rural sites, but this outcome was not surprising because  $C_{mH}$  takes into account taxon density, which often is extremely variable among riffles along a stream (Brooks et al. 2002, Blakely and Harding 2005, Heino et al. 2005). Decreased  $S$  and increased  $C_p$  in urban headwater streams suggested that headwater communities become less-diverse subsets of downstream communities as taxa are lost after urbanization.

That is, the low-diversity communities in urban headwater streams consisted mostly of taxa found in their respective main-stem reaches.

The RDA also indicated greater similarity between headwater and main-stem communities in rural sites than urban sites (Fig. 5). Stream/reach type significantly influenced taxonomic composition of insect communities at rural sites (pairwise RDAs; Fig. 5). Rural headwater communities, defined by taxa such as *D. modesta*, *Dolophilodes* (Trichoptera:Philopotamidae), *Leuctra*, and *Dicranota* (Diptera:Tipulidae), were different from rural main-stem reach communities, which were defined by taxa such as *Hydropsyche bronta* (Trichoptera:Hydropsychidae), *Cheumatopsyche*, and

TABLE 3. Taxa found in the headwater stream that were not in the main-stem reach in the same site.

Taxon		Rural			Urban			
		R-DRK	R-MPE	R-SNC	U-RBR	U-SAL	U-SPD	
Ephemeroptera	Baetidae	<i>Acerpenna</i> sp.						
		<i>Fallceon</i> sp.	X					
	Ephemerellidae	<i>Ephemerella</i> sp.	X					
		<i>Serratella</i> sp.						
Odonata	Tricorythidae	<i>Tricorythodes</i> sp.						
	Cordulegastridae	<i>Cordulegaster</i> sp.	X	X				
		Coenagrionidae	<i>Argia</i> sp.		X			
	Calopterygidae	<i>Ischnura</i> sp.					X	
<i>Calopteryx maculata</i>						X		
Plecoptera	Leuctridae	<i>Leuctra</i> sp.		X				
	Chloroperlidae	<i>Suwallia</i> sp.						
		Perlidae	<i>Eccoptura xanthenes</i>		X			
		<i>Perlesta</i> sp.						
Hemiptera	Veliidae	<i>Microvelia</i> sp.	X	X				
		<i>Rhagovelia</i> sp.						
	Corydalidae	<i>Nigronia serricornis</i>						
		<i>Nigronia fasciatus</i>		X				
Trichoptera	Sialidae	<i>Sialis</i> sp.						
	Hydropsychidae	<i>Ceratopsyche slossonae</i>						
		<i>Diplectrona modesta</i>	X	X				
	Odontoceridae	<i>Psilotreta</i> sp.		X				
Lepidostomatidae	<i>Lepidostoma</i> sp.		X					
Limnephilidae	<i>Pycnopsyche</i> sp.		X					
Philopotamidae	<i>Dolophilodes</i> sp.							
Polycentropodidae	<i>Cyrnellus</i> sp.		X					
	<i>Polycentropus/Cernotina</i>							
	Psychomyiidae	<i>Lype diversa</i>		X				
	Rhyacophilidae	<i>Rhyacophila</i> sp.	X					
	Uenoidae	<i>Neophylax concinnus</i>	X	X				
		<i>Neophylax oligius</i>	X					
Coleoptera	Dryopidae	<i>Neophylax mitchelli</i>		X				
Diptera	Tipulidae	<i>Helichus</i> sp.		X				
		<i>Dicranota</i> sp.						
		<i>Hexatoma</i> sp.	X	X				
		<i>Limnophila</i> sp.		X				
		<i>Molophilus</i> sp.		X				
		<i>Ormosia</i> sp.		X				
		<i>Pseudolimnophila</i> sp.		X				
		<i>Pilaria</i> sp.		X				
		<i>Tipula</i> sp. 1						
		<i>Tipula</i> sp. 1						
		<i>Tipula</i> sp. 1						
		Culicidae	<i>Aedes</i> sp.					
		Dolichopodidae						
		Ephydriidae						
	Dixidae	<i>Dixa</i> sp.	X	X				
	Empididae	<i>Chelifera</i> sp.	X					
		<i>Clinocera</i> sp.	X	X				
	Stratiomyidae	<i>Nemotelus</i> sp.		X				
		<i>Odontomyia</i> sp.						

TABLE 3. Continued.

Taxon			Rural			Urban		
			R-DRK	R-MPE	R-SNC	U-RBR	U-SAL	U-SPD
Diptera	Ceratopogonidae	<i>Alluaudomyia</i> sp.		X				
		<i>Atrichopogon</i> sp.	X					
		<i>Bezzia-Palpomyia</i> complex	X					
	Tabanidae	<i>Ceratopogon</i> sp.		X				
		<i>Culicoides</i> sp.		X				
		<i>Chrysops</i> sp.	X	X	X			
	<i>Hybomitra</i> sp.		X					
Taxa restricted to the headwater stream			19	34	29	4	1	2
Total taxa in the headwater stream			42	59	46	21	6	7

*Antocha* (Diptera:Tipulidae) (Fig. 5). In contrast, stream/reach type did not influence taxonomic composition of insect communities at urban sites (pairwise RDAs; Fig. 5). This result suggests that taxonomic composition of urban headwater and main-stem reach communities was similar. Moreover, urban and rural main-stem communities had similar taxonomic composition, whereas urban and rural headwater communities differed (Fig. 5). Thus, the relevant taxonomic changes must have occurred in the urban headwater communities.

#### Potential causes

*Habitat degradation.*—Riparian deforestation resulting from watershed urbanization can alter the taxonomic composition of stream communities (Sweeney 1993, Wallace et al. 1997). In deforested streams, the trophic structure of the headwater community may change from the shredder-based community expected in small forested streams to one based on functional feeding groups expected in higher-order streams (Sweeney 1993, DeLong and Brusven 1998, Meyer and Wallace 2001). This shift in trophic structure could cause shifts in taxonomic composition that might increase similarity between headwater and main-stem communities. However, the extensive riparian deforestation that would cause this type of change in trophic structure did not occur in our urban headwater watersheds (Table 2), and the only functional feeding group that differed between rural and urban headwater streams was predators. Thus, it is unlikely that deforestation was the cause of the shift in taxonomic composition of urban headwater communities.

Poor water or habitat quality probably contributed to the loss of unique headwater taxa in urbanized headwater streams. Most taxa that were eliminated from urban headwater streams were sensitive to pollution, but some pollution-sensitive taxa (tolerance value  $\leq 2$ ; Stribling et al. 1998), such as *Glossosoma*

(Trichoptera:Glossosomatidae), *Dolophilodes*, *Oulimnius latiusculus* (Coleoptera:Elmidae), and *Ancyronyx* (Coleoptera:Elmidae), did persist in urban headwater streams. Thus, urban headwater communities were not solely a subset of the most-tolerant taxa found in rural headwaters. Moreover, our measures of water and habitat quality were not markedly different between urban and rural headwater streams. Conductivity and pH were not statistically different between the urban and rural headwater streams. Silt was sometimes the dominant substrate type at individual transects in some urban headwater streams, but the substrate was primarily cobble in these streams. A more-open canopy could have caused some sensitive taxa to be eliminated from urban headwater streams (Sweeney 1993). Riparian canopy cover was lower in urban than in rural sites, but the difference was not enough to affect trophic structure and probably not enough to affect overall taxonomic composition. Thus, water and habitat quality were probably not the sole causes of the shift in taxonomic composition in urban headwater streams.

*Effects of land use.*—An effort was made to select rural and urban sites with similar amounts of urbanization in the watersheds of the main-stem reaches. However, the occurrence of urbanization in a headwater watershed usually was associated with urbanization in the main-stem watershed. As a result, main-stem watersheds in urban sites generally were more urbanized than main-stem watersheds in rural sites (Table 1). Thus, in urban sites, urbanization might have affected headwater streams and main-stem reaches similarly. Also, urban main-stem watersheds were generally smaller than rural main-stem watersheds and thus potentially more similar to the headwater streams. As a result, urban headwater streams and main-stem reaches might have been more physically similar than rural headwater streams and main-stem reaches. This similarity might have led to

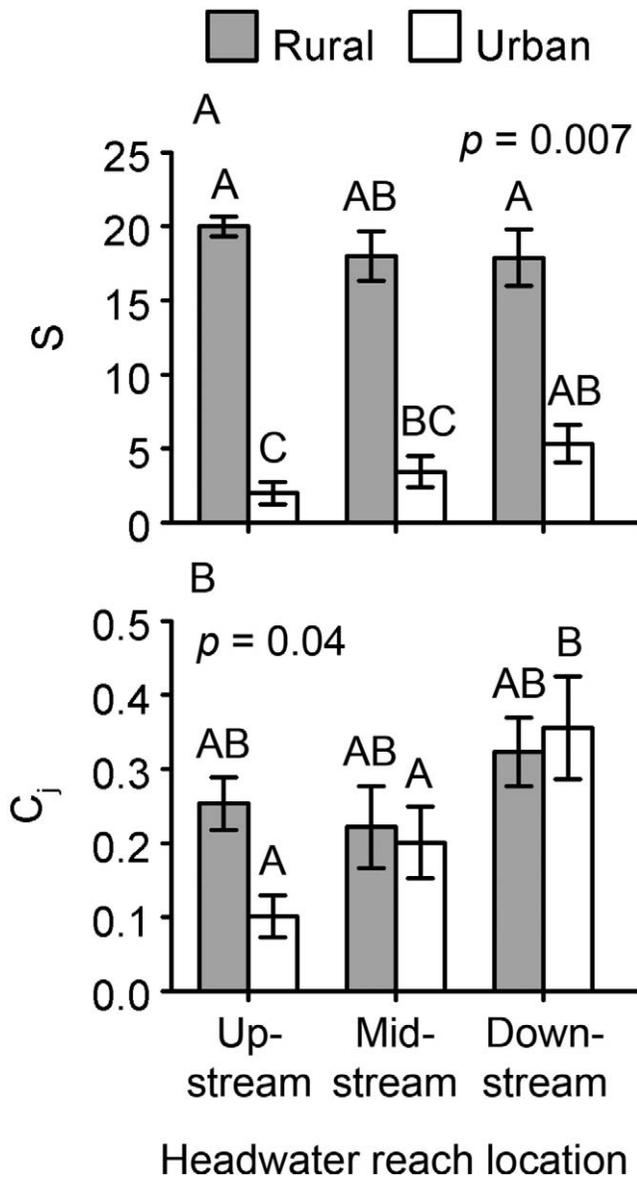


FIG. 6. Mean ( $\pm 1$  SE) number of taxa ( $S$ ) in upstream, midstream, and downstream reaches in rural and urban headwater streams (A), and mean ( $\pm 1$  SE) Jaccard index ( $C_j$ ) values calculated between communities in the main-stem reach and each headwater reach in rural and urban sites (B).  $p$  is the probability associated with the land use type  $\times$  reach position interaction (analysis of variance). Bars with the same letters are not significantly different (Tukey–Kramer adjustment).

greater taxonomic similarity among urban headwater and main-stem communities than rural communities.

*Longitudinal patterns.*—Longitudinal patterns of  $S$  and  $C_j$  differed between urban and rural headwaters, such that  $S$  and  $C_j$  were highest in downstream reaches of urban headwater streams and did not differ between upstream and downstream reaches in rural

headwater streams (Fig. 5). These results suggest that proximity to the main stem might have influenced longitudinal patterns of taxonomic composition. Longitudinal differences in water and habitat quality were not thoroughly measured at our sites and might have affected longitudinal patterns of community composition. However, the short length of headwater streams and the lack of lateral inputs from other streams made large longitudinal differences in water and habitat quality unlikely. Our results suggest that urbanization affected the composition of stream insect communities in ways not fully explained by degradation of habitat and water quality. Headwater communities could have become similar to main-stem communities if the main stem acted as the primary source of insect immigrants, and the longitudinal patterns of  $S$  and  $C_j$  partially support this theory.

Headwater streams lack drifting or crawling immigrants and must rely primarily on oviposition by adult females for recruitment (Mackay 1992, Moser and Minshall 1996, Bunn and Hughes 1997, Humphries 2002, Elliot 2003). Piping headwater streams underground (Meyer and Wallace 2001), decreasing the pool of potential immigrants at a watershed scale (Briers et al. 2002), or anthropogenic structures that attract adult immigrants to terrestrial habitats (Kriska et al. 1998) might limit immigration from other headwater streams. If this were the case, more main-stem immigrants would have reached downstream than upstream reaches of urban headwaters, with the result that  $S$  and  $C_j$  would have been higher in downstream than in upstream headwater reaches. Longitudinal dispersal barriers, such as road culverts, could have produced the same patterns (Blakely et al. 2006) but were present on only one urban headwater stream. Thus, a lack of immigrants from surrounding headwaters might have contributed to the overall similarity in addition to habitat degradation.

*Summary*

Urbanization decreased  $S$  of insect communities in headwater streams, and the taxa that were lost after urbanization were mostly those unique to headwater communities in rural watersheds. Previous work has established that degraded water and habitat quality resulting from watershed urbanization decreases  $S$  of aquatic insect communities (Paul and Meyer 2001). Our study showed that the community remaining in urban headwater streams was mostly a subset of the community found downstream in the main-stem reach. This result corroborates the conclusions of other studies that taxa unique to headwaters are at the greatest risk of local extirpation after watershed

urbanization, and that these habitats should be given priority for conservation and restoration (Meyer and Wallace 2001, Meyer et al. 2007).

Patterns of taxon loss in urban headwater streams suggest that degradation of local water and habitat quality is the most likely determinant of insect community composition in urban headwater streams. However, effects of urbanization on the terrestrial environment can alter regional processes, such as dispersal, and might influence community composition in urban headwaters (Sanderson et al. 2005). If the patterns in our study were the result of limited dispersal from adjacent headwaters and continued migration from the main-stem reach, then community composition in the main stem could have mediated the response of urban headwater communities to water- and habitat-quality degradation. Thus, species distributions, dispersal abilities of individuals, proximity to potential sources, and species density in source populations should be considered when designing conservation or restoration projects for headwater streams (Fuchs and Statzner 1990, Whiles and Wallace 1992, Palmer et al. 1997, 2005, Ahlroth et al. 2003, Bond and Lake 2003). The patterns we found warrant further research to determine the extent that insect community composition is influenced by the effect of urbanization on terrestrial environments.

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