

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 ²)	% urban	% agriculture	% forest	Watershed area (km ²)	% 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 ^a	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 ^b	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

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

^b Urban area is underestimated because of new construction not in GISHydro2000 (2nd 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 2nd- 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 (2nd 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-m² 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

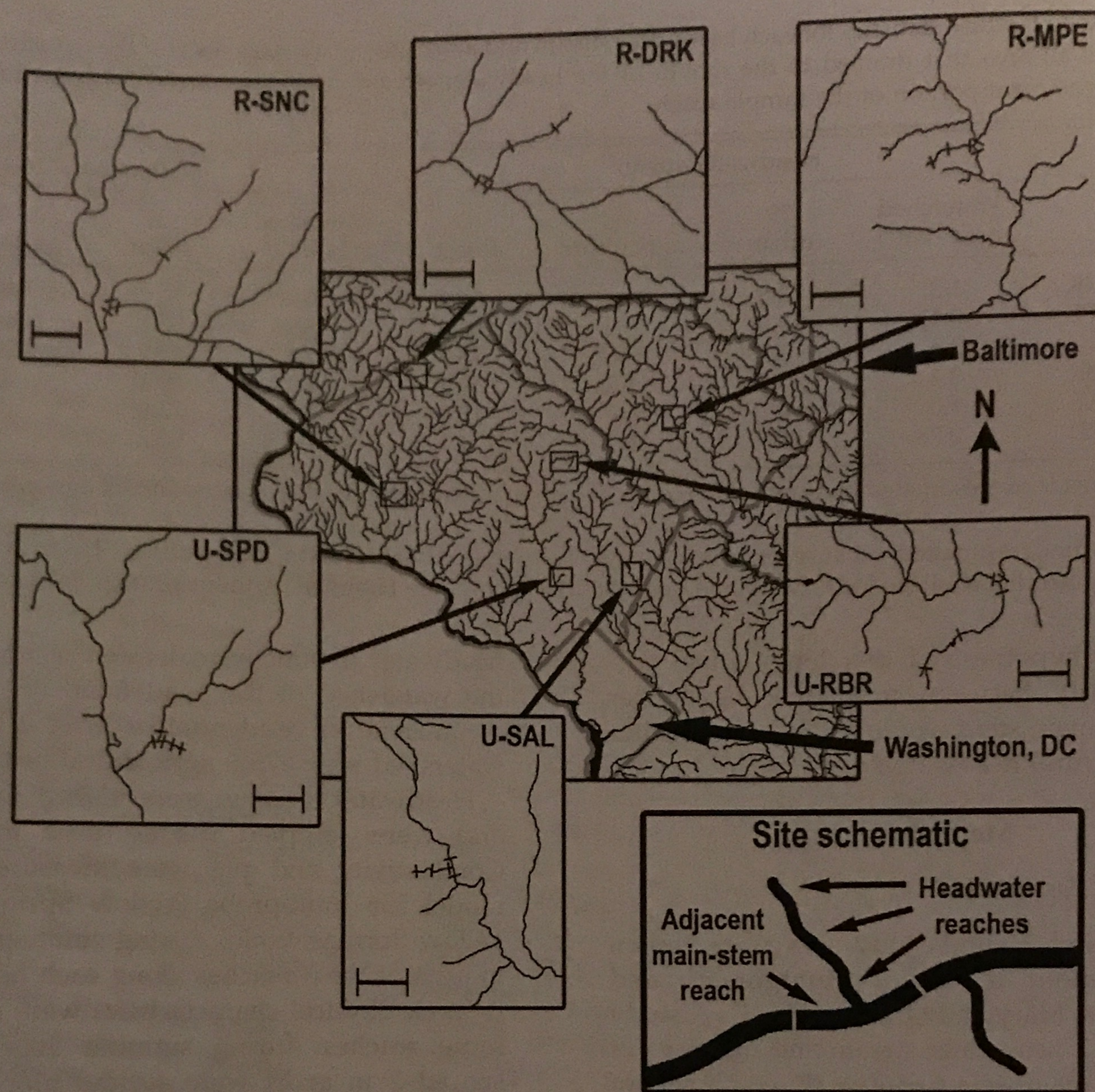


FIG. 1. Study sites in Montgomery and Howard counties, Maryland. The site schematic on the bottom right shows a generalized view of the sampling locations within a site. Sites consisted of a headwater stream and its adjacent main-stem reach. The adjacent main-stem reach is the reach on the higher-order 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-m² Surber sampler (mesh size = 250 μ m) 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 $\geq 80\%$). 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 $\arcsine(\sqrt{x})$ -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 Smilauer 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-m² 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 ³ /s)	Slope ^a (%)	Width ^b (m)	Depth ^b (cm)	Dominant substrate	Canopy cover ^a (%)	Conductivity ^a (mS/cm)	pH ^a
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	$p = 0.05$	NA	$p = 0.05$	NS	NS

^a Mean of 3 reaches

^b 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_j* and *C_{mH}* 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_j* and *C_{mH}* values calculated between individual headwater reaches and the composited main-stem communities were subplots within urban and rural site whole plots. Mean *S* was log₁₀(*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 km² to 3.4 km² (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 km² to 162.1 km². 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 ($F_{1,4} = 20.85$, $p = 0.01$; Fig. 2A) and *H'* ($F_{1,6.35} = 45.68$; $p = 0.0004$; Fig. 2B) were significantly lower and mean *D* ($F_{1,5.14} = 18.92$, $p = 0.007$; Fig. 2C) was significantly greater in urban than rural headwater

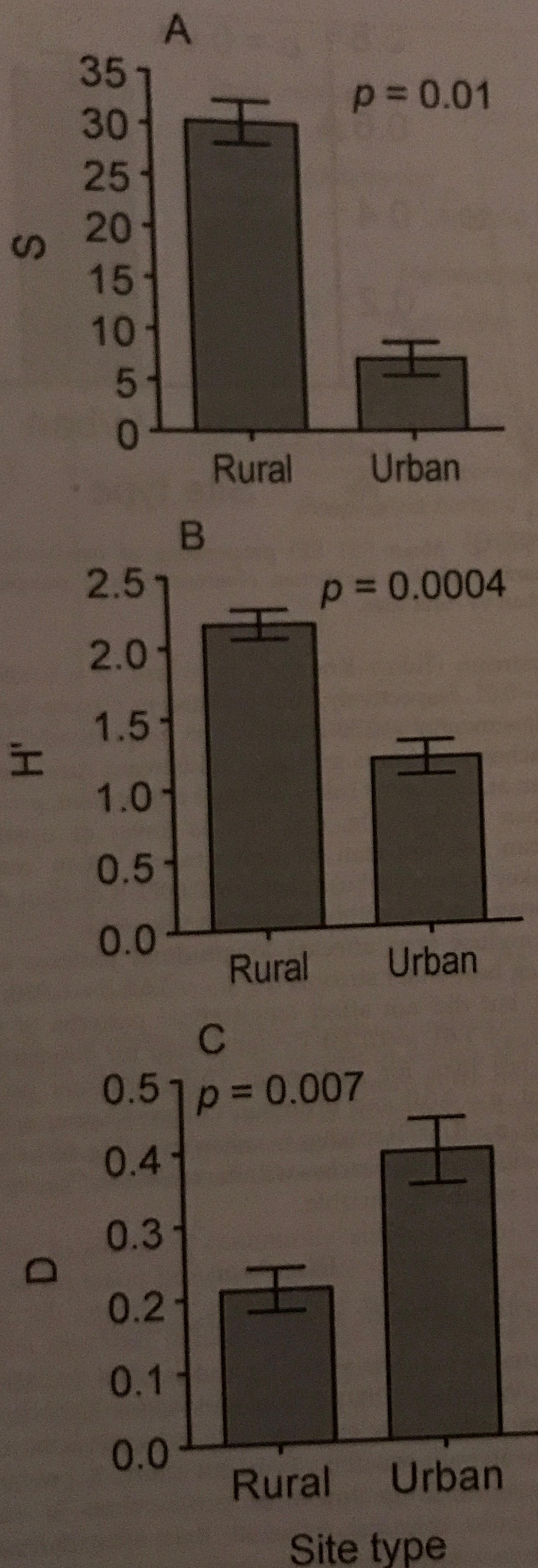


FIG. 2. Mean (± 1 SE) taxonomic richness (S) (A), Shannon diversity index (H') (B), and Simpson's diversity index (D) (C) for rural and urban headwater streams.

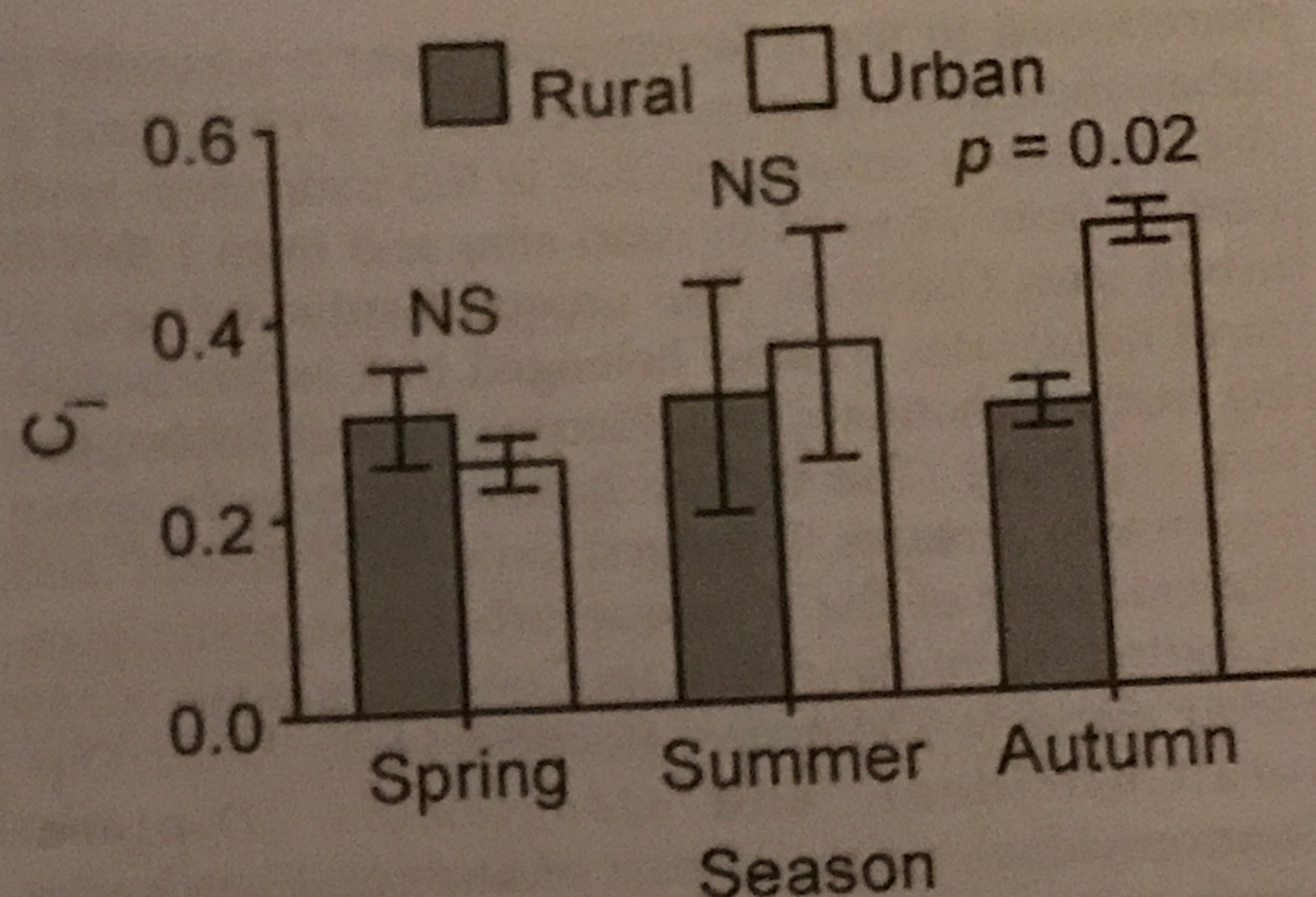


FIG. 3. Mean (± 1 SE) Jaccard index (C_j) for each season for urban vs rural sites. NS = rural and urban sites not significantly different within a season.

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