

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 1st axis explained 89.5% of the total residual variance explained by stream/reach type, and the 2nd 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 1st axis. Urban headwater and main-stem and rural main-stem communities were separated along the 2nd 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

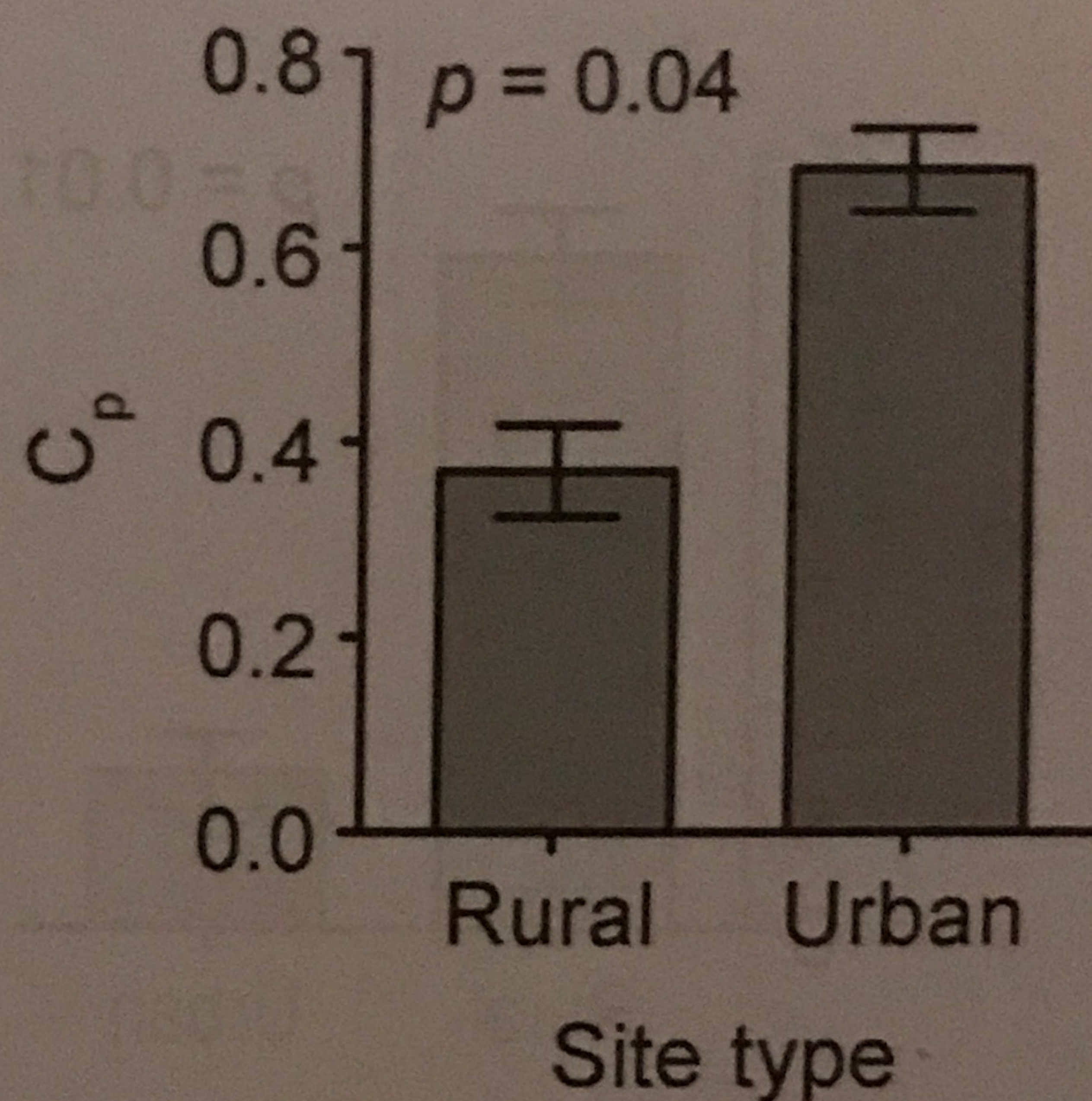


FIG. 4. Mean (± 1 SE) proportions of headwater taxa shared with the main-stem community (C_p) sampled for urban vs rural sites.

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).

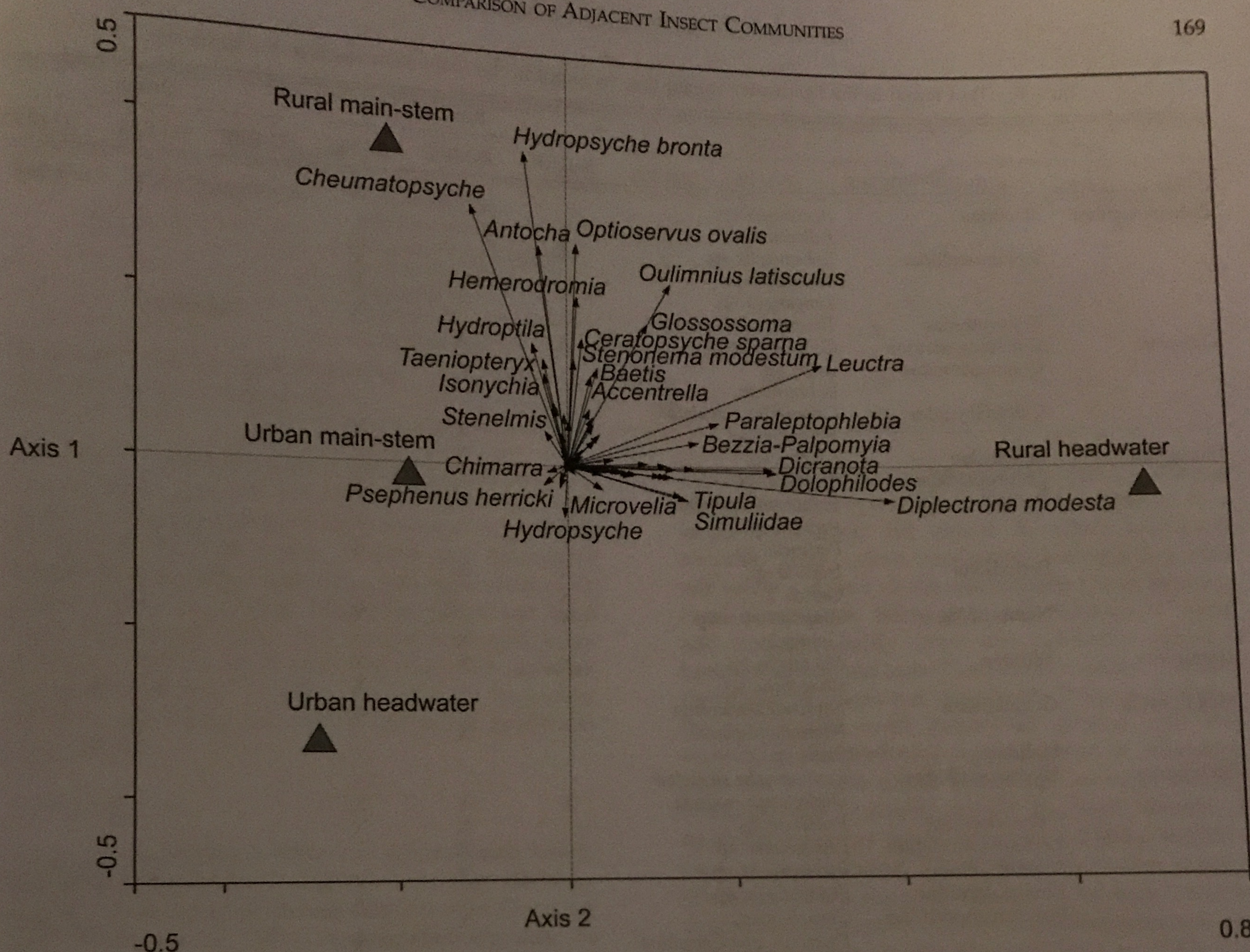


FIG. 5. Biplot resulting from redundancy analysis including all 4 stream/reach types (urban and rural headwater and urban and rural main stem). Taxa are represented by vectors, and stream/reach types are represented as centroids (triangles). The distance between centroids represents the difference in 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 1st axis explained 89.5% of the total residual variance explained by stream/reach type and the 2nd 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

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						
Ephemereilidae						
Tricorythidae						
Cordulegastridae						
Coenagrionidae						
Calopterygidae						
Leuctridae						
Chloroperlidae						
Perlidae						
Perlodidae						
Nemouridae						
Veliidae						
Corydalidae						
Sialidae						
Hydropsychidae						
Odontoceridae						
Lepidostomatidae						
Limnephilidae						
Philopotamidae						
Polycentropodidae						
Psychomyiidae						
Rhyacophilidae						
Uenoidae						
Dryopidae						
Tipulidae						
Coleoptera						
Diptera						
Culicidae						
Dolichopodidae						
Ephydriidae						
Dixidae						
Empididae						
Stratiomyidae						

TABLE 3. Continued.

Diptera	Taxon	Rural						Urban		
		R-DRK	R-MPE	R-SNC	U-RBR	U-SAL	U-SPD			
Ceratopogonidae	<i>Alluaudomyia</i> sp.		X							
	<i>Atrichopogon</i> sp.	X								
	<i>Bezzia-Palpomysia</i> complex	X								
	<i>Ceratopogon</i> sp.		X							
	<i>Culicoides</i> sp.		X							
	<i>Chrysops</i> sp.		X							
Tabanidae	<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 ≤ 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 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

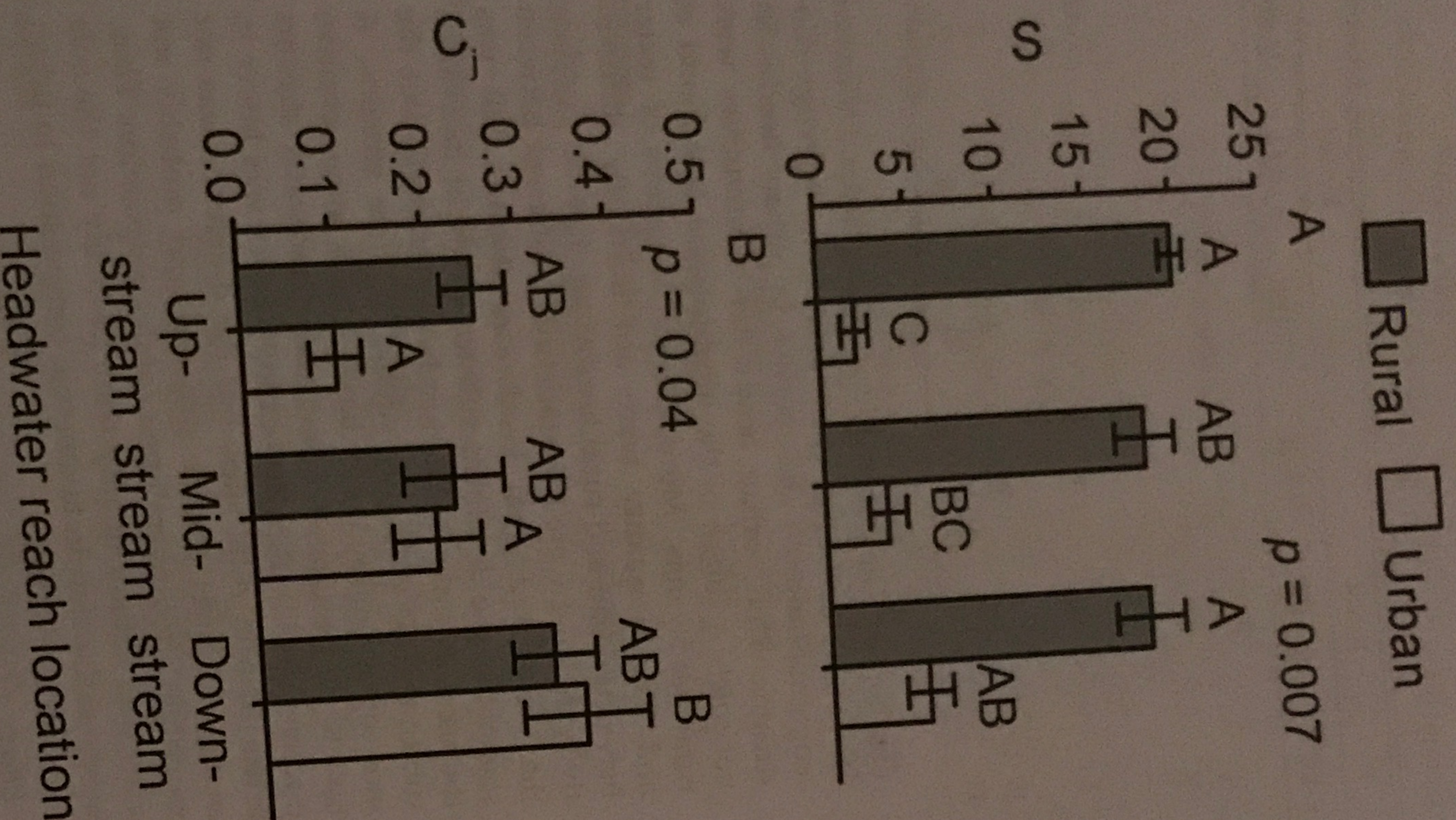


FIG. 6. Mean (± 1 SE) number of taxa (S) in upstream, midstream, and downstream reaches in rural and urban headwater streams (A), and mean (± 1 SE) Jaccard index (C_j) values calculated between communities in the main-stem reach and each headwater reach in rural and urban sites (B). p is the probability 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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