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Interregional variation in urbanization-induced geomorphic change and macroinvertebrate habitat colonization in headwater streams

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Abstract. Urban land use alters channel morphometry, particle size structure, and sediment-transport dynamics in stream ecosystems, thereby degrading the habitat of aquatic organisms. However, stream form varies substantially among geoclimatic settings, and, thus, the degree of negative effects induced by urbanization may be region-specific. Biota in streams of the Coastal Plain ecoregion of the eastern US consistently show greater tolerance to urban land use than do biota of the adjacent Piedmont, potentially because of a disparity in geomorphic degradation between ecoregions. We quantified channel morphometry, particle mobility, sediment deposition, and floodwater chemistry in similarly sized rural and urban streams of both ecoregions to detect differences in urbanization-induced geomorphic change. Macroinvertebrate rates of recolonization in patches of disturbed benthic habitat also were monitored. No differences in channel morphometry were observed among treatment groups. Riffle particle sizes were significantly larger in urban than in rural Piedmont streams, but a corresponding disparity was absent in Coastal Plain streams. Particle mobility increased in urban settings uniformly between ecoregions. However, transported particles were substantially larger in Piedmont streams. Sediment deposition was higher overall in Coastal Plain streams but more affected by urbanization in Piedmont streams. Macroinvertebrate density in the disturbed habitat rose faster over time in Coastal Plain than in Piedmont streams. Results suggest that geomorphic degradation is greater in Piedmont streams and that organisms may be adapted to benthic instability in Coastal Plain streams. In addition, our findings demonstrate that ecosystem-scale responses of streams to urbanization may vary inherently among geoclimatic settings.

Key words: urbanization, geomorphology, physiography, colonization, Mid-Atlantic.

Urbanization induces substantial geomorphic adjustment and, consequentially, benthic habitat alteration in streams. Decades of empirical studies have led to the creation of a predictive temporal framework of sediment deposition and channel morphometry dynamics following watershed urbanization (Paul and Meyer 2001, Walsh et al. 2005). Construction activity initially causes a pulse of hillslope-sediment delivery and consequential aggradation, which is followed by an indefinite period of reduced deposition and loss of fine sediment once urban expansion ceases (Wolman 1967, Allmendinger et al. 2007, Colosimo and Wilcock 2007). The ultimate reduction in fine sediments occurs because an increase in floods of moderate magnitude causes effective downstream transport of movable particles (Pizzuto et al. 2000). Because of the eventual relative paucity of fine sediments and simultaneous increase in scouring flow events, active channels in urban streams typically increase in bankfull width or become incised (Gregory et al. 1992, Van Duin and Garcia 2006, Hardison et al. 2009).

However, characteristic stream form and function vary substantially among landscapes, so the severity of geomorphic adjustment following urbanization may vary as well. Stream hydrology, morphometry, and benthic sediment composition are naturally structured by local geoclimatic attributes, such as topographic relief, geologic setting, and climate (Rosgen 1996, Faustini et al. 2009). Interregional comparisons show that such diversity in stream form probably leads to differences in the degree of geomorphic degradation in urbanized settings. For instance, streams in the Central Great Plains and Central Basin/Range North American ecoregions may show no signs of channel enlargement following

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watershed urbanization (Short et al. 2005, Kang and Marston 2006). Furthermore, the proportion of benthic sediments composed of fine particles may increase over time in certain urban streams because of prolonged bank erosion (Short et al. 2005, Allmendinger et al. 2007), whereas in other streams, sediment composition may remain relatively unchanged (Kang and Marston 2006). Therefore, both the magnitude and nature of geomorphic responses to urbanization are heterogeneous among stream forms.

Aquatic biota might exhibit variable sensitivity to urbanization across stream forms because of differences in geomorphology. Physical disturbance induced by hydrologic adjustment often is identified as the mechanistic driver of declining biotic integrity in urban streams (Roy et al. 2005, Knight et al. 2008). However, lotic organisms possess behavioral adaptations to cope with natural flood events (Bunn and Arthington 2002), and the success of such strategies in urban-affected streams may be related to the extent of habitat degradation. For example, aquatic invertebrates take refuge in patches of woody-debris snags during elevated flows (Palmer et al. 1996, Angradi 1997, Hax and Golladay 1998), and wood abundance might decrease (Larson et al. 2001), remain unchanged, or increase (Short et al. 2005) once streams are urbanized. In addition, benthos inhabiting stream beds composed of large, stable particles tend to recover from floods more rapidly than benthos in reaches composed of small, transportable material (Cobb et al. 1992, Imbert et al. 2005). Despite such observations, efforts to deduce if certain geomorphic settings confer biotic tolerance to urbanization are absent.

The Coastal Plain and adjacent Piedmont ecoregions of eastern North America are an example of interregional variation in stream ecosystem-scale sensitivity to urbanization. Recent bioassessments at the community (Morgan and Cushman 2005, Goetz and Fiske 2008, Cuffney et al., in press) and taxon-specific (Utz et al. 2009, 2010) scales demonstrate greater biological intolerance to urbanization in the Piedmont than in the Coastal Plain or other ecoregions. Subsequent complementary studies revealed differences in thermal and hydrologic responses of streams to urbanization between ecoregions (Utz et al., in press). Specifically, the frequency, magnitude, and duration of flood events all change to a relatively greater degree along gradients of urbanization in the Coastal Plain than in the Piedmont, although Piedmont streams are inherently more prone to intense flooding when rural sites are compared. In contrast, mean and event-related temperatures are more affected in the Piedmont. Characteristic stream geomorphology varies substantially between ecoregions. Thus, geomorphic responses to urbanization also may be region-specific. Morphometric and sediment-regime alteration in urban streams have been explored separately in both ecoregions (i.e., Leopold 1973, Allmendinger al. 2007, Hardison et al. 2009), but studies that explicitly compare the degree of effect between ecoregions have not been conducted.

To determine whether geomorphic adjustment caused by urbanization varies between Coastal Plain and Piedmont streams, we quantified morphology and sediment-transport dynamics in rural and urban watersheds in both ecoregions. We considered features presumed to be temporally static after an initial geomorphic-adjustment phase in urban streams (e.g., bankfull width, depth, and sediment structure) and temporally dynamic attributes, such as sediment stability and deposition. We also monitored macroinvertebrate recolonization in physically disturbed habitat patches to detect interregional differences in how benthic communities respond to disturbance. Because patterns in biological responses to urbanization are disparate, we hypothesized that geomorphic degradation would be more pronounced in urban Piedmont than in urban Coastal Plain streams. Furthermore, we predicted that macroinvertebrate recolonization of disturbed habitat would occur more rapidly in Coastal Plain than in Piedmont streams.

Methods

Study region

The Coastal Plain and eastern Piedmont physiographic regions are hydrogeomorphically distinct. Elevation in the Coastal Plain is <100 m, and topography ranges from rolling hills with deeply incised stream channels to almost uniformly flat (Thornbury 1965). Basement rock is buried at depths of 10 to 1000 m below unconsolidated to semiconsolidated crystalline particles and a relatively thick, permeable layer of soil (Markewich et al. 1990, Ator et al. 2005). Streams tend to be low-gradient with cobble, gravel, sand, and silt dominating benthic sediments. In contrast, Piedmont elevations range from 60 to >500 m in some locations, and most watersheds feature undulating ridges and valleys. Consolidated basement rock in the Piedmont lies beneath 1 to 2 m of soil with some exposed outcropping at higher elevations and in stream channels (Swain et al. 2004). Dominant benthic sediments in the Piedmont range from boulder to gravel, and stream gradients are generally steeper than those in the Coastal Plain. The boundary between the 2 ecoregions extends from New Jersey to Alabama (Fig. 1), but we limited our study to sites in Maryland

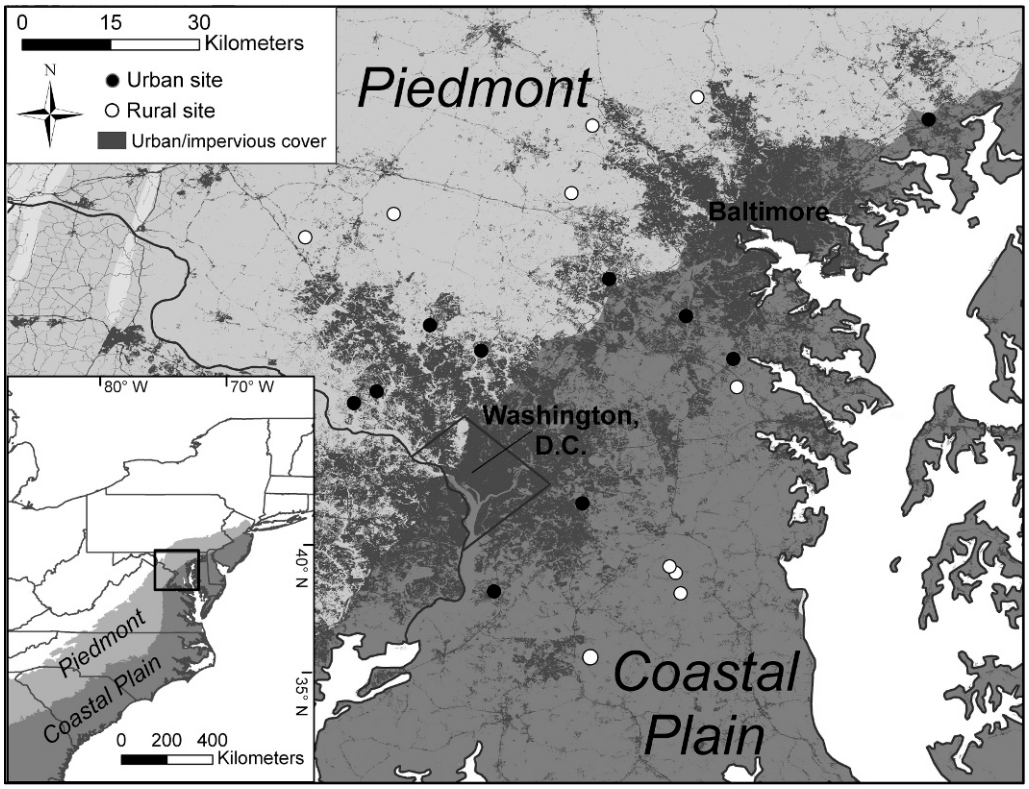

FIG. 1. Map showing study sites, Coastal Plain and Piedmont physiographic ecoregions of the eastern US, and metropolitan centers in the regions.

because we had access to a large database of watershed attributes within the state.

Benthic macroinvertebrate community composition differs between the 2 ecoregions. Macroinvertebrate assemblages in the Coastal Plain tend to be uniquely dissimilar to those in nearby ecoregions, possibly because of a high diversity of stream types within the ecoregion (Feminella 2000). In Maryland, total faunal diversity probably is greatest in this ecoregion (Utz et al. 2009). Certain stream types in the Coastal Plain support distinct assemblages (e.g., blackwater streams; Smock and Gilinsky 1992), but these stream types were not included in study sites. The diversity and abundance of flies (particularly chironomids), amphipods, dragonflies, and mollusks tends to be higher in Coastal Plain streams, whereas Piedmont streams typically have relatively more diverse and abundant populations of stoneflies and caddisflies (Feminella 2000, Utz et al. 2009). Some taxa, such as the net-spinning caddisflies *Hydropsyche* and *Chimarra* and the mayfly *Stenonema*, are common in both ecoregions.

Site selection

A database of watershed-scale information on each 75-m reach of stream in the state of Maryland (developed at the University of Maryland Center for Environmental Science, Appalachian Laboratory) was referenced to select study sites. Impervious surface cover (%, hereafter ISC) and Anderson 1st-level landuse classes were quantified at the watershed- and 200-m riparian-buffer scale by overlaying catchment and riparian-area boundaries with the 2001 National Land Cover Database (USEPA 2010) and extracting the relevant data. Only watersheds that were 1.0 to 3.5 km^2 in area and that were entirely within the Piedmont or Coastal Plain west of the Chesapeake Bay were included as candidates. Among these candidates, sites with <0.5% ISC at the watershed- and riparian-buffer scale were considered for rural sites and all watersheds with 10 to 15% ISC at both spatial scales were considered for urban sites.

After narrowing the potential pool of study sites based on the above criteria, 5 urban and 5 rural sites in each ecoregion were randomly chosen (n = 20 sites total) for possible inclusion in the study. The watershed of each selected site was visually assessed via satellite images taken during 2007, and construction permits for 2008 (MDP 2008) were checked to ensure that urban development had not ensued since 2001 nor was planned for the near future. Sites with

TABLE 1. Mean (±1 SE) values for study-site attributes. Land-cover values are percentages at the watershed scale unless otherwise noted. ISC = impervious surface cover.

Variable	Rural sites		Urban sites	
	Coastal Plain	Piedmont	Coastal Plain	Piedmont
Watershed size (km^2)	2.4 ± 0.7	2.5 ± 0.7	2.9 ± 0.7	3.0 ± 0.2
Slope (%)	0.6 ± 0.1	1.3 ± 0.3	1.0 ± 0.2	0.8 ± 0.2
% ISC	0.3 ± 0.1	0.3 ± 0.1	14.9 ± 1.3	13.8 ± 0.8
200-m riparian-buffer-scale ISC	0.1 ± 0.0	0.0 ± 0.0	12.4 ± 0.8	12.3 ± 0.9
% agriculture	35.2 ± 8.8	34.2 ± 10.1	11.1 ± 3.8	21.1 ± 4.29
% forest	59.9 ± 7.5	53.8 ± 6.6	36.8 ± 8.3	27.7 ± 3.1
% wetlands	2.4 ± 1.9	0.7 ± 0.3	1.5 ± 1.0	0.3 ± 0.2

high agricultural cover (>75% at either spatial scale) and Coastal Plain sites where benthic sediment consisted entirely of sand and silt were excluded. The sites selected for the study are shown in Fig. 1, and watershed attributes among urban/rural and ecoregions are provided in Table 1. Rural study watersheds tended to be far from and urban sites close to the physiographic divide because major metropolitan regions of Maryland (Baltimore, Washington, DC) are positioned between the 2 ecoregions.

Morphometric and sediment surveys

Channel morphometry was quantified during summer of 2008. At each site, 10 cross sections were profiled at intervals spaced ~10× the channel width apart using a surveyor's level and stadia rod (Harrelson et al. 1994). Mean bankfull width and height were derived from profiles by plotting cross sections in HEC-RAS 4.0 (USACE 2008) and estimating the extent of the active channel for each cross section. Slopes were also quantified from these measurements. Active channel cross-section area was calculated by multiplying width by height. Site-specific averages of all aforementioned variables were averaged across cross sections. Counts of large woody debris delineated into size classes based on diameter and length were conducted within the entire extent of cross sections (a distance ~100× the channel width) as outlined by Stevenson and Bain (1999).

Wolman pebble counts (Potyondy and Hardy 1994) were used to quantify benthic sediment structure. The intermediate axes of 200 randomly selected riffle sediment particles were recorded at each site. Cumulative frequency distributions derived from these data were used to determine site-specific median, 75th-, and 90th-percentile particle sizes (D_{50}, D_{75} and D_{90}).

Sediment movement and deposition

Sediment stability, deposition, and suspended/dissolved transport during flood events were measured over a 4-mo period. Five site visits spaced ~3 wk apart (anticipated precipitation occasionally delayed collection events) between October 2008 and February 2009 were made during baseflow conditions to collect data for each of the 3 procedures described below.

Bed stability was quantified using tracer-sediment movements following the methods of Townsend et al. (1997). At each site, painted particles corresponding to the local D_{75} and D_{90} (10/size class) were deployed in a line perpendicular to flow within a riffle reach that was >10 m long. The starting point was marked with surveying flags secured above the bank. During each subsequent visit, the distance of each transported particle was recorded and those displaced or lost were replaced (at the starting point). A scoring system was derived to quantify bed stability: 0 = unmoved particles, 1 = movement <1 m, 2 = movement between 1 and 10 m, and 3 = particle not recovered. The total score per size class per visit per site was summed as a measure of bed stability. Movement scores were averaged between D_{75} and D_{90} groups per visit per site because preliminary analyses demonstrated that differences in scores between size classes were negligible.

Sediment deposition was estimated by deploying passive in situ traps (Hedrick et al. 2005). The trap design consisted of a 5-cm-long piece of 10.16-cm-diameter schedule-40 polyvinyl chloride (PVC) pipe that was capped on one end, placed in an anchoring structure and filled with 12- to 25-mm painted marble particles (anchor rocks). Sediment traps were buried with the tops level with the surface of the hyporheic zone of wetted riffles. During each site visit, traps were lifted from the housing unit and the contents were collected. Samples were dried in an oven at 60°C for 120 h, the anchor rocks were removed from the dried samples, and the remaining sediments were weighed. The remaining sediments were sorted into 6 size classes through stacked sieves (8-, 4-, 2-, 1-, 0.5-, and 0.25-mm mesh) on a mechanical shaker, and the mass of each size class was recorded. Total mass and

median particle size (by mass) was quantified for each sample. In addition, the proportional volume of available space filled by deposited sediments (V) was determined using the equation:

$$V = \frac{\frac{\text{mass}_{\text{sample}}}{1.7\text{g/cm}^3}}{405.2\text{cm}^3 - \frac{\text{mass}_{\text{anchor rock}}}{2.6\text{g/cm}^3}}$$

where 1.7 g/cm^3 is the density of dry sand and gravel of mixed rock composition, 405.2 cm^3 is the trap volume, and 2.6 g/cm^3 is the density of marble (material densities were determined from dried representative samples in the laboratory).

Floodwater suspended and dissolved-solid concentrations were sampled with passive water collection during elevated flows (Schoonover et al. 2007). Collection devices consisted of 500-mL plastic bottles with a 3-mm-diameter water-intake hole near the top of the bottle and a 2-mm-diameter hole in the lid. A piece of iron rebar was secured in the stream bed and bottles were fastened to the rebar with hose clamps and cable ties. At the time of deployment, intake holes were 15 cm above the baseflow water level. If a bottle was filled during the 3-wk interim period, we collected and replaced it. Total suspended and dissolved solid (TSS and TDS, respectively) concentrations were measured in the laboratory. Conductivity and Cl^- concentrations were measured to permit comparisons of floodwater chemistry with respect to these common urban water-quality indicators. Because of the small area of the bottle intake/outtake holes (~10 mm^2), cold temperatures during the study duration, and short maximum time that a filled bottle might have been deployed prior to collection (~3 wk), it was assumed that evaporation from collection bottles was minimal (>90% of collected bottles were either entirely filled or empty when collected).

Benthic macroinvertebrate colonization

Benthic macroinvertebrate recolonization was quantified within a patch of physically disturbed benthic sediment habitat at each site. Multiple habitat types (such as debris dams) might be important to benthic macroinvertebrates, but sampling was limited to benthic substrate habitat for several reasons. The particle size, movement, and deposition dynamics investigated in our study reflected conditions experienced by organisms inhabiting benthic substrate habitat. The volume of habitat sampled across all sites could be controlled using equivalently sized baskets. Last, Coastal Plain sites were restricted to those with abundant riffle habitat and gravel–cobble-dominated benthic sediments to ensure that benthic habitat was similarly structured between ecoregions. Uniform patches of habitat were created by filling 25 × 25 × 5-cm-mesh (12-mm grade) baskets with local sediments. One basket/site was filled with wetted channel sediment and placed in a riffle between 2 and 3 February. These baskets served as control patches at the end of the study. On 3 and 4 March, 4 treatment baskets/site were filled with channel sediments, rigorously shaken while submersed in stream water, moved to the stream bank, and further disturbed by pouring ~30 L of water through the contents from a vertical distance of 0.75 m. Each basket was then buried level with the wetted-riffle hyporheic zone. One randomly selected treatment basket was removed from the channel after 3, 6, 12, or 24 d. Contents were collected using a D-net. Contents of the control basket also were collected 24 d after the treatment baskets were set (53 d since deployment). Samples were preserved in 70% ethanol. All macroorganisms other than Oligochaete worms were sorted from debris, and each individual was identified to genus except for Chironomidae (identified to subfamily).

Statistical analyses

Two-factor analysis of variance (ANOVA) models were used to test for differences among treatment groups. The 3 model components were an ecoregion term, a rural/urban dichotomous class term, and an ecoregion × rural/urban interaction term. If the interaction term proved not to be statistically significant, it was removed from the model and the remaining terms were tested in the subsequent model. Variables assumed to be related to watershed size (i.e. bankfull width, height and cross-section area) were standardized by dividing the measure by watershed area (km^2). Repeated-measures analysis of covariance (ANCOVA) models with collection events randomly blocked were used to test variables assessed on multiple visits (e.g., sediment deposition). Data were checked for normality by visually inspecting normal probability plots and using Shapiro-Wilk tests (Zar 1999). Where data were deemed not normal, $\log_{10}(x)$-transformations were used except for proportional variables bounded by 0 and 1 (i.e., proportion of available trap volume filled by deposited sediments). These data were arcsine$\sqrt{(x)}$-transformed (Zar 1999). Tukey's post hoc comparisons were used for all models quantifying geomorphic and physical differences between treatments to determine pairwise differences in means among groups.

Macroinvertebrate recolonization was assessed with a mix of univariate and multivariate techniques

TABLE 2. Mean (±1 SE) values of channel morphometric variables. Bankfull width, height, and cross-sectional area were standardized by watershed area (km^2), and large woody debris scores were standardized by transect length (m). No significant statistical differences were detected among groups.

	Rural sites		Urban sites	
Variable	Coastal Plain	Piedmont	Coastal Plain	Piedmont
Bankfull height (m)	0.8 ± 0.2	0.4 ± 0.1	0.6 ± 0.2	0.4 ± 0.1
Bankfull width (m)	3.4 ± 0.7	3.3 ± 0.7	2.6 ± 0.7	2.9 ± 0.2
Cross-sectional area (m^2)	5.7 ± 2.1	2.7 ± 0.6	3.4 ± 1.1	3.8 ± 0.4
Large woody debris score	0.9 ± 0.1	1.0 ± 0.2	0.9 ± 0.1	0.5 ± 0.1

coupled with the statistical approach described above. $Log_{10}(x)$-transformed macroinvertebrate abundance in all collections were ordinated in a nonmetric multidimensional scaling (NMS) system to measure community similarity among baskets. Rare taxa present in <5% of all baskets were excluded from the NMS analysis. The NMS system allowed us to quantify community taxonomic similarity (by abundance) in each treatment basket relative to macroinvertebrate communities in the control baskets. Colonization rates of macroinvertebrates in treatment baskets were quantified with 2 metrics: 1) the total density of all organisms, which allowed taxonomically independent assessment of habitat use, and 2) Euclidean distance in NMS space relative to communities in the corresponding control baskets. The latter measure was based on the assumption that treatment-basket NMS coordinates would become similar to the corresponding control-basket values over time. Both metrics were compared in a repeated-measures ANOVA with ecoregion, rural/urban classification, and an interaction term as class variables. Relative density was arcsine$\sqrt{(x)}$-transformed for statistical comparisons because it was bounded by 0 and 1. All linear models were run with the GLM or MIXED procedures in SAS (version 9.1; SAS Institute, Cary, North Carolina) and NMS was run in PC-Ord (McCune and Mefford 2006).

Results

Channel morphometry and sediment structure

No differences in channel morphometry were detected between ecoregion and rural/urban groups (Table 2). ANOVA models for watershed-size-standardized $log_{10}(x)$-transformed bankfull height ($F_{3,16}$ = 0.7, p = 0.558), bankfull width ($F_{3,16}$ = 0.2, p = 0.885), $log_{10}(x)$-transformed cross-sectional area ($F_{3,16}$ = 0.7, p = 0.589), and $log_{10}(x)$-transformed large woody debris abundance ($F_{3,16}$ = 2.3, p = 0.120) were not significant.

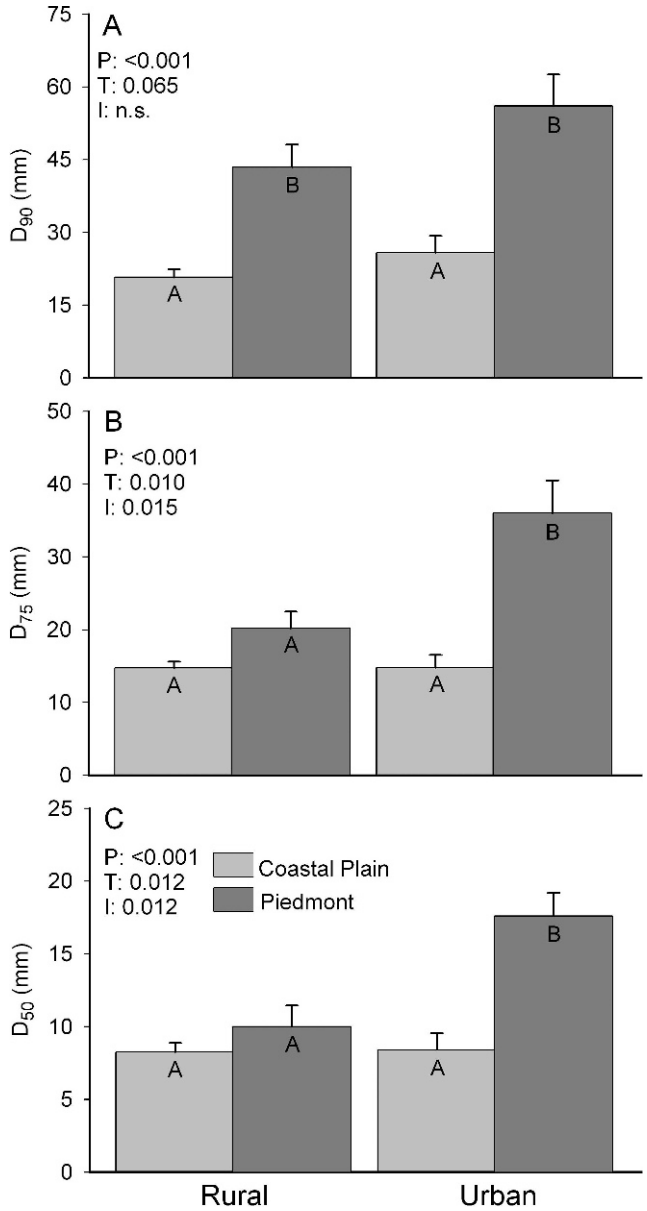

FIG. 2. Mean (±1 SE) particle diameters at the 90th (D_{90}) (A), 75th (D_{75}) (B), and 50th (D_{50}) (C) percentiles in rural and urban streams in the Coastal Plain and Piedmont ecoregions of the eastern US. p-values are shown for an analysis of variance testing for effects of ecoregion (P), urban vs rural class (T), and the ecoregion × urban/rural class interaction (I). Bars with the same uppercase letters are not significantly different. n.s. = not significant.

Benthic particle sizes varied among treatment groups, but differences between urban and rural streams were detected only in the Piedmont (Fig. 2A–C). Overall

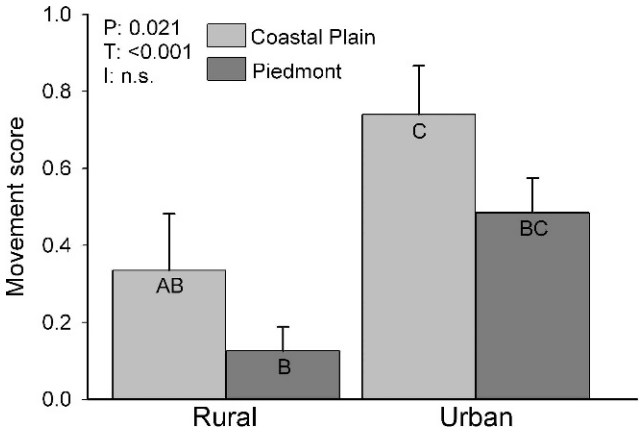

FIG. 3. Mean (±1 SE) sediment movement scores in rural and urban streams in the Coastal Plain and Piedmont ecoregions of the eastern US. *p*-values are shown for an analysis of variance testing for effects of ecoregion (P), urban vs rural class (T), and the ecoregion × urban/rural class interaction (I). Bars with the same uppercase letters are not significantly different. n.s. = not significant.

ANOVA models for all 3 assessed percentiles (D_{50}: $F_{3,16} = 11.1, p < 0.001$; D_{75}: $F_{3,16} = 12.7, p < 0.001$; D_{90}: $F_{3,16} = 12.0, p < 0.001$) were significant. As expected, Piedmont particle sizes were significantly larger than Coastal Plain particles. Urban Piedmont streams had significantly greater particle sizes compared to rural Piedmont sites for 2 size classes (D_{50} and D_{75}; Fig. 2B, C). However, particle sizes in Coastal Plain streams did not differ between urban and rural sites.

Sediment movement and deposition

Tracer-particle movement scores varied among treatment groups (Fig. 3). Large particles moved significantly further downstream in Coastal Plain than in Piedmont streams and in urban than in rural streams. However, this trend probably is partially a result of the particle-size differences between ecoregions (i.e., D_{75} and D_{90} were both greater in the Piedmont than in the Coastal Plain). The increase in movement scores between rural and urban sites did not differ between ecoregions (nonsignificant interaction term).

Water quality during floods varied among groups. However, statistical comparisons may have been compromised by the disparity in sample sizes between rural and urban sites (Table 3). Twelve samples were collected from rural sites compared to 39 from urban sites. Nevertheless, significant differences were detected among treatment groups for some water-quality variables. TSS concentrations did not differ significantly between ecoregions or urban and rural streams ($p > 0.05$ for all 3 model terms), although values from urban sites tended to be higher than values from rural sites. The urban/rural ($F = 15.9, p < 0.001$) and interaction ($F = 6.48, p = 0.015$) terms of the TDS model were significant, but the ecoregion term was not ($F = 0.0, p > 0.05$). $\text{Log}_{10}(x)$-transformed conductivity ($F = 17.9, p < 0.001$) and $\log_{10}(x)$-transformed Cl^- ($F = 7.0, p = 0.011$ were significantly higher in urban than rural sites, but the remaining terms were not statistically significant for either variable. However, post hoc comparisons suggested that Cl^- concentrations and conductivity were elevated in urban streams of the Coastal Plain (Table 3).

The amount and size of sediment passively collected by traps differed significantly among treatment groups. The total mass of deposited sediments (Fig. 4A) and the proportion of available trap volume filled by deposited sediments (Fig. 4B) was significantly higher in Coastal Plain than in Piedmont streams. Both variables were significantly greater in urban than in rural streams, but only in the Piedmont. The D_{50} of deposited sediments was significantly higher in Piedmont streams than in Coastal Plain streams and was higher in urban than in rural streams (Fig. 4C). However, the interaction term for the median particle size model was not statistically significant.

Benthic macroinvertebrate colonization

A 2-dimensional NMS ordination system (stress = 14.7) of macroinvertebrate community composition

TABLE 3. Mean (±1 SE) values for floodwater chemistry variables. Means with the same uppercase letters are not significantly different.

	Rural sites		Urban sites	
Variable	Coastal Plain	Piedmont	Coastal Plain	Piedmont
Number of filled bottles	5	7	20	19
Total suspended solids (mg/L)	247.2 ± 90.9	293.9 ± 91.8	507.2 ± 73.7	407.3 ± 67.6
Total dissolved solids (mg/L $\times 10^{-1}$)	0.8 ± 0.1^{A}	1.2 ± 0.2^{AB}	2.3 ± 0.4^{C}	1.5 ± 0.1^{B}
Conductivity	78.5 ± 21.5^{A}	146 ± 8.9^{AB}	412 ± 115.6^{C}	223.7 ± 23.3^{BC}
Cl^- (mg/L)	13.4 ± 2.9^{A}	20.4 ± 3.2^{AB}	71.5 ± 24.1^{B}	34.7 ± 6.2^{AB}

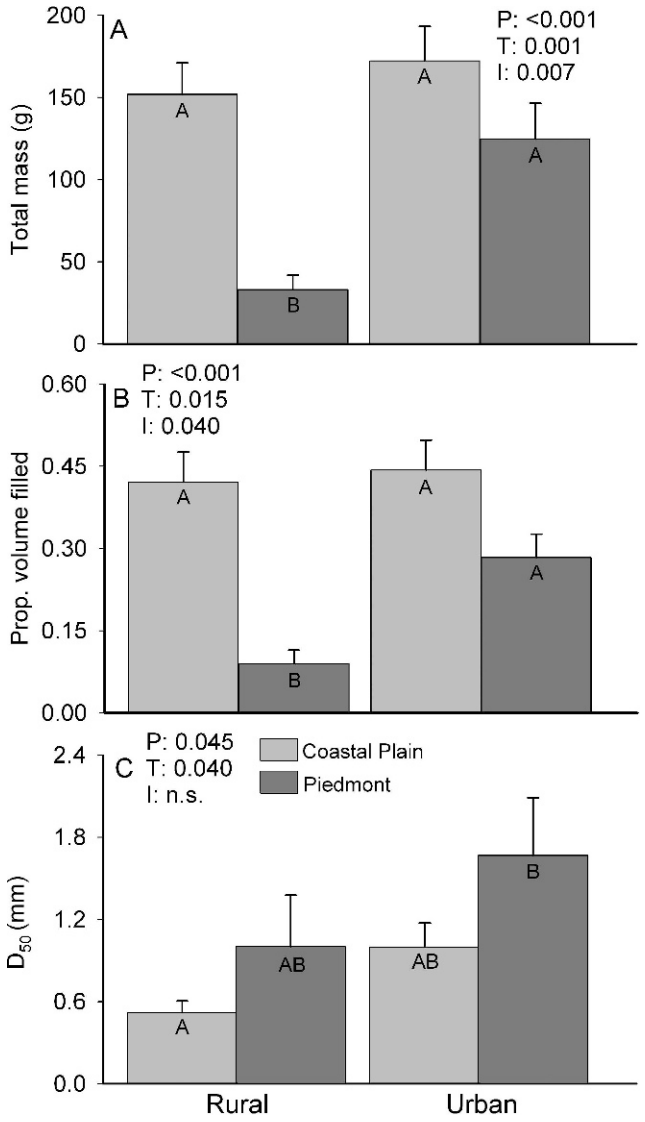

FIG. 4. Mean (±1 SE) mass (A), proportion of available trap volume filled by deposited sediments (B), and median particle size (D_{50}) (C) of sediments collected by passive in situ sediment traps in rural and urban streams in the Coastal Plain and Piedmont ecoregions of the eastern US. *p*-values are shown for an analysis of variance testing for effects of ecoregion (P), urban vs rural class (T), and the ecoregion × urban/rural class interaction (I). Total mass was $\log_{10}(x)$-transformed and the proportion of available trap by deposited sediments was arcsine$\sqrt{(x)}$-transformed prior to statistical comparisons. Bars with the same uppercase letters are not significantly different. n.s. = not significant, prop. = proportion.

revealed differences in assemblage structure among treatment groups (Fig. 5). Communities in rural streams differed distinctly between the Coastal Plain and Piedmont, whereas communities in urban streams were similar between ecoregions. Rural

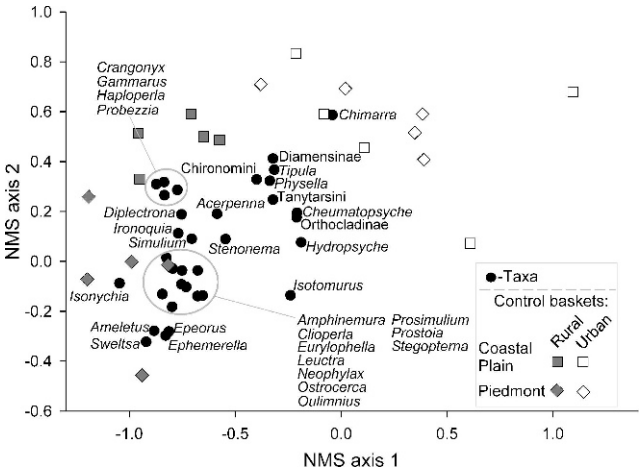

FIG. 5. Nonmetric multidimensional scaling (NMS) plot of scores for macroinvertebrate communities in control baskets and weight-averaged taxon scores. Treatment baskets (not shown) also were included in the ordination system. Only taxa for which ≥30 individuals were collected among all baskets are shown.

Piedmont streams were characterized by high abundances of the mayfly genera *Ameletus*, *Epeorus*, and *Ephemerella* and stonefly genera *Sweltsa* and *Prostoia* (Fig. 5). Rural Coastal Plain streams were characterized by varying abundances of amphipods (*Crangonyx* and *Gammarus*), the stonefly *Haploperla*, and the ceratopogonid *Probezzia*. Urban streams in both ecoregions were characterized by high abundances of chironomids and the caddisfly *Chimarra*. Some taxa, such as the stonefly *Amphinemura* and the mayfly *Ephemerella*, appeared consistently in treatment baskets collected early during the colonization period, but no taxa seemed to be specifically associated with early stages of substrate colonization.

Recolonization of habitat as quantified by NMS community similarity suggested that macroinvertebrate communities rebounded more rapidly from physical disturbance in rural than in urban streams (Fig. 6A). Communities in treatment baskets were more similar to communities in control baskets at early stages in rural Coastal Plain streams than in other streams, but no statistically significant difference was detected between ecoregions. In contrast, both ecoregion and urban/rural class terms were significant in the macroinvertebrate density model. Densities in treatments increased faster relative to in control baskets in Coastal Plain than in Piedmont streams (Fig. 6B). Densities in rural Coastal Plain streams were nearly 50% higher in the 24-d treatment baskets relative to in control baskets, whereas densities in rural Piedmont streams remained ~50% lower in the 24-d treatment baskets relative to in

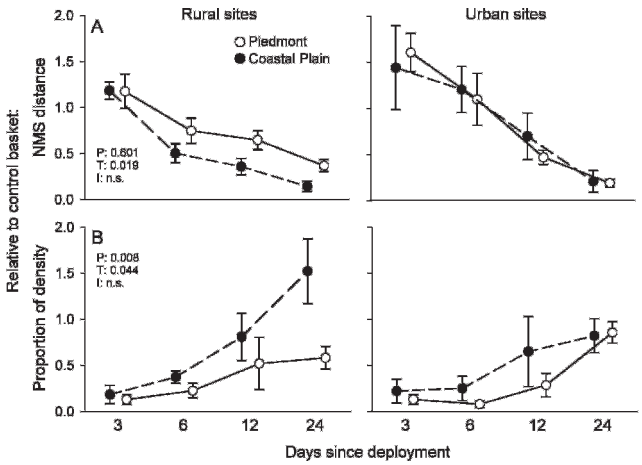

FIG. 6. Mean (±1 SE) Euclidean distances in nonmetric multidimensional scaling (NMS) space based on taxonomic abundance data (A) and density in treatment baskets relative to control baskets as a function of days since deployment (B) in rural and urban streams in the Coastal Plain and Piedmont ecoregions of the eastern US. *p*-values are shown for an analysis of variance testing for effects of ecoregion (P), urban vs rural class (T), and the ecoregion × urban/rural class interaction (I). Relative density was arcsine$\sqrt{(x)}$-transformed prior to statistical comparisons. n.s. = not significant.

control baskets. Similar ecoregion-specific differences in recolonization measured by density also were detected in urban streams, but the disparity was not as pronounced as in rural sites.

Discussion

As predicted, ISC-induced geomorphic degradation was more severe in Piedmont streams than in Coastal Plain streams. The interregional disparity was particularly acute for variables associated with sediment structure, stability, and large-particle movement. Benthic sediments were more unstable and prone to transport in rural Coastal Plain streams than in any other stream type. However, sediment deposition and particle size were significantly greater in urban than in rural Piedmont streams, whereas no such differences were detected in Coastal Plain streams. Furthermore, the increase in D_{75} and D_{90} particle movement between rural and urban streams was uniform between ecoregions (Fig. 3), but the corresponding particle sizes were much greater in the Piedmont, and particularly in urban Piedmont streams (Fig. 2A–C). Thus, when particle movement and the corresponding particle size are considered simultaneously, the disparity between rural and urban sites in ability to transport large sediment was substantially greater in the Piedmont.

Our results contribute to related work suggesting that streams with fine sediments in watersheds of low topographic relief are inherently less prone than streams with coarse sediments or high topographic relief to geomorphic change in urban settings. Low-gradient, sand/silt bottom streams in Oklahoma (Kang and Marston 2006) and Georgia (Riley 2009) showed no signs of channel enlargement or changes in threshold grain size (particle size assumed to be at the threshold of motion; Kang and Marston 2006) in urban vs rural settings, but Hardison et al. (2009) reported heightened channel incision in urban Coastal Plain streams. One reason why sediment-structure change does not occur in the Coastal Plain might be related to available streambed material. The large particles that dominate urbanized streams in other systems are not present in Coastal Plain channels. Furthermore, riparian wetlands tend to be more extensive in lowland ecosystems and might mitigate the hydrologic effects of urbanization (Burns et al. 2005, Riley 2009) by reducing the effects of urbanization on geomorphic and physicochemical properties. Regardless of the mechanism, biotic resilience to urban land use appears to be consistently greater in low- than in high-gradient streams (Snyder et al. 2003, Utz et al. 2009), perhaps because habitat alteration is relatively less severe in low-gradient streams.

Macroinvertebrate recolonization of disturbed habitat appears to occur more rapidly in Coastal Plain than in Piedmont streams. Total densities in Coastal Plain treatment baskets far exceeded those in control baskets after 24 d, and treatment baskets were colonized more rapidly in rural Coastal Plain than in rural Piedmont streams when taxon-specific abundances were considered (but this difference was not statistically significant). Thus, benthos in Coastal Plain streams might be relatively better dispersers and more opportunistic colonizers of hyporheic habitat. Spatial scale and likelihood of local adaptation must be considered when interpreting such results. Recolonization of invertebrate fauna following disturbance was faster in stream beds with large particles than in stream beds with finer particles (Cobb et al. 1992, Nislow 2002, Imbert et al. 2005). However, these studies were conducted at a small spatial scale in watersheds with uniform geoclimatic conditions. In contrast, organisms in separate ecoregions (e.g., Coastal Plain vs Piedmont) probably are adapted to local disturbance regimes (Mackay 1992), and in particular, Coastal Plain macroinvertebrates may be adapted to unstable sediments.

Rapid colonization following disturbances might render Coastal Plain benthic fauna relatively more tolerant than Piedmont fauna to urbanization, but

additional studies are required to test this hypothesis. Macroinvertebrate densities in Coastal Plain urban streams rebounded from physical disturbance more rapidly than those in Piedmont urban streams. Furthermore, many taxa that were distinctly associated with Coastal Plain sites (i.e., *Crangonyx*, *Gammarus*, *Probezzia*, and chironomids) are inherently more tolerant of urbanization than the highly urban-sensitive stonefly and mayfly genera that characterize typical Piedmont streams (Utz et al. 2009). However, we investigated colonization ability in only one habitat (benthic substrate of riffles). Riffle substrate is considered a fundamental habitat for many invertebrates and, therefore, is often sampled for interregional comparison studies (Cuffney et al., in press). However, other habitats, such as debris dams, probably are important refuges for macroinvertebrates during high flows (Palmer et al. 1996, Hax and Golladay 1998). Interregional differences in habitat use might contribute to disparities in community-scale tolerance of urbanization among other ecoregions, especially if a particular habitat is important during flood disturbances. Regardless of the mechanism, macroinvertebrates appear to vary among ecoregions in tolerance to urbanization (Utz et al. 2009, Cuffney et al., in press), and differing degrees of habitat alteration among ecoregions might be a contributing mechanism behind these trends.

Our finding that channel morphometry did not differ between urban and rural or Coastal Plain and Piedmont streams contrasts with the results of most related studies. Stream channels in hydrogeomorphic settings similar to the Coastal Plain might not typically enlarge as a consequence of urbanization, but Piedmont streams consistently exhibit widening or incision in urban settings (Pizzuto et al. 2000, Allmendinger et al. 2007, Colosimo and Wilcock 2007). Furthermore, Coastal Plain streams are expected to possess naturally smaller bankfull widths and heights per unit of watershed area than are Piedmont streams (Johnson and Fecko 2008). Why we did not detect similar differences in sites between rural and urban settings or physiographic ecoregions is not clear, but one potential explanation might be the spatial scale of the study. Sites were separated by distances $>\sim 100$ km and included a range of channel slopes (Fig. 1, Table 1). Therefore, stream morphometry could have varied partially as a consequence of local nuances in landform.

A number of factors should be recognized when interpreting our results. First, we did not consider the structural arrangement and direct connectivity of ISC to stream channels, but such information typically is pertinent when deducing effects in urban streams (Booth and Jackson 1997, Walsh et al. 2009). Chemical analyses of flood water suggested that connectivity might have been greater in Coastal Plain urban streams, where the geomorphic effect of urbanization was relatively less severe than in Piedmont urban streams. Second, sites in the Coastal Plain were selected only if stream beds were dominated by relatively large particles (cobble, gravel, and sand). However, many Coastal Plain streams possess sediment structures composed exclusively of sand or finer materials, such as silt and clay. Whether observed effects of urbanization would have differed in streams with relatively fine sediments is not known. Third, microclimatic differences among sites might have resulted in variable disturbance regimes. However, we sampled in autumn and winter specifically to avoid confounding effects of intense local storms that most often occur during summer. The proportion of bottles filled among treatments suggests that precipitation variability was similar across the study region. Last, we measured recolonization after simulated disturbance in small patches rather than observing dispersal following an actual storm. Thus, the behavior of benthos following whole-stream-scale disturbance might differ from that reported, particularly in potentially critical habitats associated with organic debris, such as debris dams (Palmer et al. 1996).

Despite the absence of morphometric variability in channels among treatments, most of our results confirm an overall difference in stream ecosystem-scale responses to urbanization between the Coastal Plain and Piedmont. Physicochemical baseline conditions and degradation along urban gradients differ between these ecoregions. Relative to rural Piedmont streams, rural Coastal Plain streams experience fewer floods that are longer in duration and smaller in magnitude. However, each of these flow-regime attributes changes significantly more along ISC gradients in the Coastal Plain than in the Piedmont (Utz et al., in press). In contrast, thermal effects along ISC gradients are significantly greater in naturally cooler Piedmont streams than in Coastal Plain streams. These trends and the observed differences in geomorphic degradation indicate that ecosystems might have unique responses to landscape stressors among ecoregions.

Hydrologic (Poff et al. 2006, Brown et al. 2009, Utz et al., in press), chemical (Sprague and Nowell 2008, Brown et al. 2009), biological (Meador et al. 2005, Potopava et al. 2005, Cuffney et al., in press), and habitat (Short et al. 2005) degradation along gradients of urbanization differ among ecoregions, and geomorphic responses to urbanization appear to be consistent with these interecoregional differences.

Despite these clear differences, generalities, such as the assertion that stream ecosystem degradation accelerates when watershed ISC reaches 10 to 15% (reviewed by Schueler et al. 2009), persist and often are assumed to apply in all situations. Results of studies based on comparative interregional approaches to understanding landscape stressors and their effects on streams increasingly indicate that these generalities are vastly oversimplified. Intensity of degradation in response to urbanization is context-dependent, and certain environmental variables might not respond uniformly among stream forms. Further study of ecoregion-scale variability in environmental degradation is warranted given the rapidly increasing proportion of streams degraded by ISC (Theobald et al. 2009) and the consequential loss of ecosystem services.

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