

Stream communities across a rural–urban landscape gradient

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ABSTRACT

Rapid urbanization throughout the world is expected to cause extensive loss of biodiversity in the upcoming decades. Disturbances associated with urbanization frequently operate over multiple spatial scales such that local species extirpations have been attributed both to localized habitat degradation and to regional changes in land use. Urbanization also may shape stream communities by restricting species dispersal within and among stream reaches. In this patch-dynamics view, anthropogenic disturbances and isolation jointly reduce stream biodiversity in urbanizing landscapes. We evaluated predictions of stream invertebrate community composition and abundance based on variation in environmental conditions at five distinct spatial scales: stream habitats, reaches, riparian corridors and watersheds and their spatial location within the larger three-river basin. Despite strong associations between biodiversity loss and human density in this study, local stream habitat and stream reach conditions were poor predictors of community patterns. Instead, local community diversity and abundance were more accurately predicted by riparian vegetation and watershed landscape structure. Spatial coordinates associated with instream distances provided better predictions of stream communities than any of the environmental data sets. Together, results suggest that urbanization in the study region was associated with reduced stream invertebrate diversity through the alteration of landscape vegetation structure and patch connectivity. These findings suggest that maintaining and restoring watershed vegetation corridors in urban landscapes will aid efforts to conserve freshwater biodiversity.

Keywords

Biodiversity, community assembly, fragmentation, metapopulation, spatial scale, urbanization.

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INTRODUCTION

During the 21st century, human populations throughout the world are expected to become more urbanized (UN Human Settlements Programme, 2004). This projection has critical implications for conservation efforts because increases in human density often are associated with loss of aquatic biodiversity (Paul & Meyer, 2001; Malmqvist & Rundle, 2002; Allan, 2004). Urbanization has been linked to declines in species diversity, trophic diversity and shifts toward more tolerant community compositions (Ourso & Frenzel, 2003; Roy *et al.*, 2003; Moore & Palmer, 2005). Urbanization also can contribute to the local extirpation and regional endangerment of native freshwater species (Frissell, 1993). Since aquatic invertebrates constitute important food web links (e.g. salmonids, Poff & Huryn, 1997) and sensitive indicators of water quality and associated ecosystem services (e.g. clean drinking water, Karr, 1999), such losses may

have substantial effects on urban ecosystems. However, attempts to predict and prevent species loss have been complicated by the multiple pathways through which urbanization can degrade streams and by the nonlinear responses of aquatic communities to urbanization (Wang *et al.*, 2001; Ourso & Frenzel, 2003; Allan, 2004). Hence, mitigating the ecological effects of rapid urbanization requires that we understand the relative contributions of the multiple mechanisms through which anthropogenic land conversion influences stream biota.

The structure of stream communities is determined by processes that operate over multiple spatial scales ranging from fine-scale habitat variation within stream reaches to coarse-scale variation among watersheds (reviewed in Vinson & Hawkins, 1998; Allan, 2004). These multiscale processes often interact, leading to hierarchical and correlated changes in stream attributes and communities (Frissell *et al.*, 1986; Poff & Huryn, 1997). Within this hierarchical framework, stream communities may be

dominated by variation at one or more scales, thus providing a focal point for limited funds for ecological research and restoration. Some studies have suggested that local instream habitat and physicochemical conditions provide the most accurate predictions of stream community structure (Roy *et al.*, 2003; Wang *et al.*, 2003; Heino *et al.*, 2004). Other studies attribute greater importance to coarser-scale riparian and watershed land use variables based on their extensive influence on stream hydrology, morphology and chemistry (Richards *et al.*, 1996; Allan *et al.*, 1997; Lammert & Allan, 1999; Wang *et al.*, 2001; Snyder *et al.*, 2003; Weigel *et al.*, 2003; King *et al.*, 2005). An emerging synthesis suggests that watershed-scale variables provide the most accurate predictions of stream communities whenever terrestrial alterations are severe enough to subsume the importance of local instream variation (Wang *et al.*, 2003; Allan, 2004).

However, urbanization not only alters instream habitat, chemistry and flow regime, but also fragments terrestrial habitat necessary for the movement and reproduction of stream invertebrates. Human-created obstructions and severe local degradation within river systems can fragment populations by imposing instream barriers to movement (Fagan *et al.*, 2002; Malmqvist, 2002). At the same time, anthropogenic land use can restrict overland dispersal of adult aquatic invertebrates (Petersen *et al.*, 1999, 2004). In this patch-dynamics view, stream reaches are enmeshed within a larger dendritic metapopulation such that the outcome of local colonization–extirpation dynamics depends on both linear (within or along streams) and lateral (among-watersheds) dispersal (Palmer *et al.*, 1996; Fagan, 2002; Malmqvist, 2002; Macneale *et al.*, 2005). Loss of connectivity can cause local extirpations either because colonization is insufficient to replace populations lost due to local disturbances (metapopulation dynamics, Palmer *et al.*, 1996; Fagan, 2002), because species become increasingly mismatched to locally dynamic communities and environments (species sorting metacommunity, Chase & Leibold, 2002) or because declining populations are no longer rescued by immigration from source habitats (mass-effects metacommunity, Mouquet & Loreau, 2002). Increasingly, patch-dynamics approaches are being applied to understand and predict variation in aquatic communities (Palmer *et al.*, 1996; Fagan *et al.*, 2002; Malmqvist, 2002; Cottenie & De Meester, 2004; Leibold & Norberg, 2004; Urban, 2004). However, to date, we know little about the effect of landscape fragmentation on stream communities in urban contexts.

We evaluated three hypotheses about the relative contributions of multiscale processes to the prediction of stream invertebrate community composition and abundance along an urbanization gradient: (1) invertebrate community structure primarily depended on direct alteration of local instream habitat and physicochemical conditions; (2) coarse-scale changes in watershed land use and riparian vegetation predicted invertebrate community structure; and (3) dispersal among stream reaches determined variation among invertebrate communities. These three hypotheses incorporated mechanisms assumed to operate over divergent spatial scales, including local instream degradation, regional alteration of land use/land cover and long-distance dispersal among stream reaches. At the same time, the study design

allowed us to contrast a niche-orientated view of environment–species relationships among heterogeneous stream patches (hypotheses 1–2) with a metapopulation view that emphasizes regional colonization–extirpation dynamics (hypothesis 3). To evaluate these hypotheses, we conducted a comprehensive survey of environmental variation associated with four spatial scales in 18 watersheds that share similar climate, topography and geology but that differ in household density (Fig. 1). Environmental variation was characterized by variables chosen a priori to reflect those most often used to predict stream invertebrate communities (Hynes, 1970; Resh & Jackson, 1993; Lamberti & Hauer, 1996; Allan *et al.*, 1997) at the scales defined by the natural extents of stream habitat units, stream reaches, riparian corridors and watersheds (Frissell *et al.*, 1986). Community structure was analysed in relation to these four spatial scales and with respect to geographical position within the larger three-river basin. We then compared the strengths of ensuing relationships to understand the relative influence of various sets of predictors on local community structure.

METHODS

Site selection

We initially generated a list of 60 candidate first- and second-order streams located within a section ($A = 679 \text{ km}^2$) of the spatially contiguous basin formed by the drainages of the West, Mill and Quinnipiac rivers into New Haven Harbor (Connecticut, USA) (Fig. 1). Eighteen tributaries from this data set were selected to represent a gradient of urbanization as measured by household density while maintaining similar size (first- or second-order), geological surficial material (glacial alluvium) and watershed area ($4.6 \text{ km}^2 \pm 50\%$).

Environmental sampling

Stream environments were characterized at four spatial scales: habitat unit, stream reach, riparian corridor and watershed, in accordance with definitions provided by Frissell *et al.* (1986). At each scale, we collected information on the environmental variables typically used to predict stream invertebrate communities based on a review of existing literature (Hynes, 1970; Resh & Jackson, 1993; Lamberti & Hauer, 1996; Allan *et al.*, 1997; Poff & Huryn, 1997; Barbour *et al.*, 1999). In total, we measured 52 physical (e.g. substrate, discharge, flow regime), chemical (e.g. nitrate, phosphate, dissolved oxygen) and ecological (e.g. riparian vegetation diversity, percent forest cover) variables (Table 1). Flow and sediment conditions within habitat units, the most commonly used categories of habitat variation in stream studies (Lamberti & Hauer, 1996; Barbour *et al.*, 1999), were collected at scales of $< 10 \text{ m}^2$. Stream reaches were characterized by physical and chemical variation (e.g. discharge, pH, nitrate concentration). We also sampled the density, diversity and composition of vegetation in a riparian corridor within 10 m of the stream bank and 150 m along each side of the bank (combined area of 3000 m^2). At the coarsest scales, watersheds were described by vegetation and land use (mean watershed area = 4.6 km^2) and their spatial locations

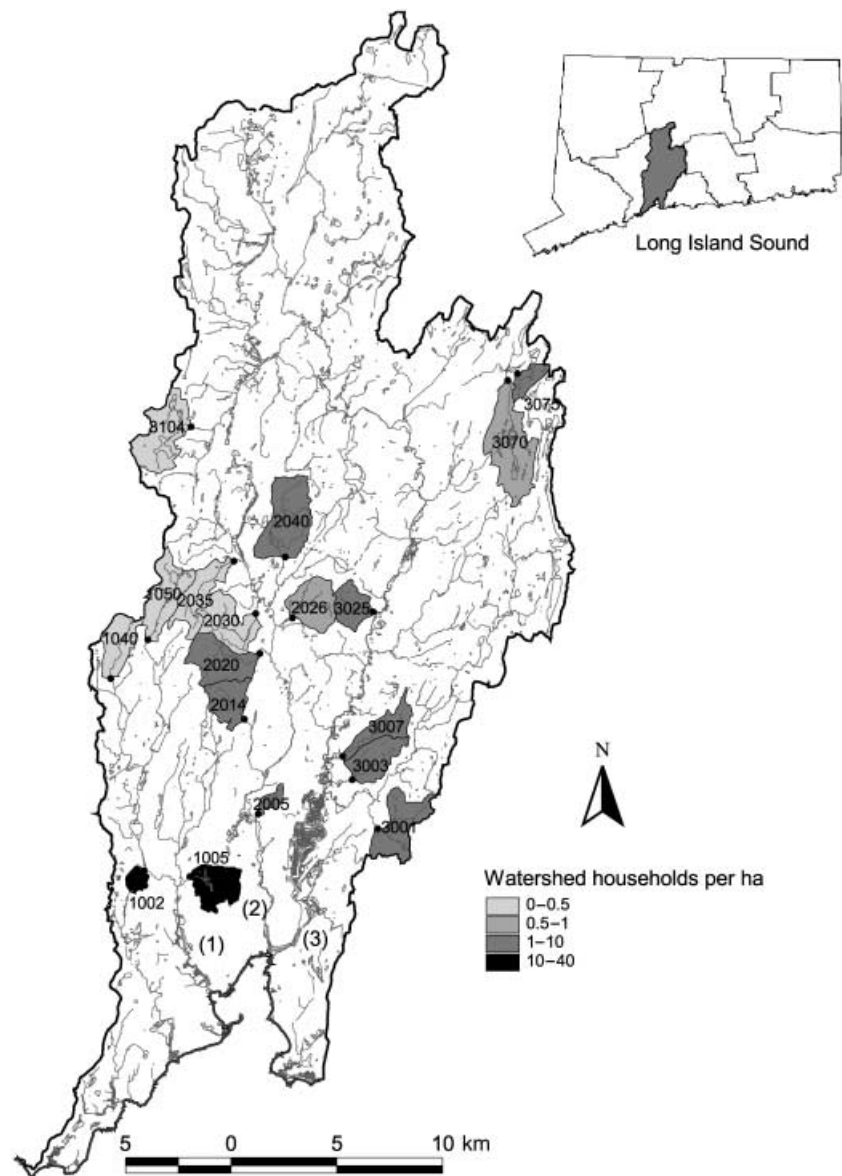


Figure 1 Map of study region in New Haven County, Connecticut, USA. Entering the New Haven Harbor on Long Island Sound are (1) the West, (2) the Mill and (3) the Quinnipiac rivers. Each of the 18 watersheds sampled in the study are identified by a unique number and their population density is indicated by differing shades of grey. Sampling points are shown by filled circles.

within the three-river basin (total basin extent = 679 km²). Hereafter, the term local will be applied to conditions experienced by stream invertebrates within a stream reach and the term regional to variation in the vegetation and land use of the surrounding terrestrial landscape.

Within each habitat unit, we measured water depth at the centre of each invertebrate sampling quadrat and qualitatively estimated percentage substrate in 5% increments according to four size categories: clay/silt/sand, gravel, cobble or boulder. At the outlet of each tributary, physicochemical variables were collected by synoptic sampling at each stream mouth on 32 sampling dates from June 1998–September 1999. Samples recorded both base-flow ($n = 20$) and stormflow ($n = 12$) conditions to amalgamate conditions experienced by invertebrate taxa over time. We measured flow via stream stage with stage-flow rating curves calculated for each tributary. Physical and chemical parameters including temperature, conductivity, suspended sediments,

nutrients, anions and faecal coliform were analysed with standard techniques (Clesceri *et al.*, 1998). Mean values for each variable were used except in the case of faecal coliform, for which the geometric mean was calculated. Riparian tree and shrub data were collected in replicated circular plots of 100 m² and 50 m², respectively, centred 5 m from the stream bank. We collected herb data from four circular 1-m² plots equidistant along the perimeter of shrub plots. Watershed land cover was determined by partitioning remotely sensed data collected in 1994–96 into 34 mutually exclusive categories. We supplemented our estimates of population density from 1990 US Census Bureau household density data by conducting a census of new housing in each watershed.

Invertebrate sampling

We assessed stream invertebrate biodiversity as the composition and abundance of taxa collected from six samples stratified

Table 1 Environmental factors and their variation across watersheds categorized by spatial scale of collection. Bold print denotes those variables selected by RDA at each spatial scale. Note that no mean or range is given for habitat types (pool, run, riffle) since their numbers were predetermined by sampling design

| | Variable | Units | Mean \pm SD | Range | |
|-----------------------------------|---|-----------------------------|-------------------|------------------|-----------|
| Local habitat | Pool | Presence | — | — | |
| | Run | Presence | — | — | |
| | Riffle | Presence | — | — | |
| | Clay/silt/sand substrate | Percent | 37 \pm 31 | 0–100 | |
| | Gravel substrate | Percent | 16 \pm 11 | 0–35 | |
| | Coarse substrate | Percent | 21 \pm 17 | 0–63 | |
| | Boulder substrate | Percent | 28 \pm 25 | 0–68 | |
| Stream reach | Mean depth | cm | 26 \pm 10 | 13–52 | |
| | Mean discharge | mm/day | 2.47 \pm 1.07 | 1.25–5.23 | |
| | Mean temperature | °C | 15.46 \pm 1.45 | 12.91–17.94 | |
| | Dissolved oxygen | Percent | 85.0 \pm 10.2 | 58.1–97.7 | |
| | Conductivity | μ mho/cm | 215 \pm 102 | 82–425 | |
| | Field pH | pH units | 7.36 \pm 0.23 | 7.07–7.83 | |
| | Turbidity | NTU | 6.91 \pm 7.45 | 1.37–34.76 | |
| | Suspended particulate matter | mg/L | 10.36 \pm 5.79 | 2.74–29.74 | |
| | Faecal coliform | No./100 mL | 539 \pm 1066 | 30–4730 | |
| | Chloride | μ M | 699 \pm 454 | 162–1730 | |
| | Nitrate | μ M | 60.0 \pm 31.3 | 10.8–113.4 | |
| | Phosphate | μ M | 0.57 \pm 0.41 | 0.18–1.82 | |
| | Sulphate | μ M | 139.7 \pm 44.8 | 89.3–251.6 | |
| | Total nitrogen | μ M | 86.3 \pm 37.7 | 21.9–157.2 | |
| | Dissolved organic carbon | μ M | 275.2 \pm 68.0 | 163.1–448.5 | |
| | Riparian Vegetation | Total tree diversity | No. | 25.17 \pm 5.83 | 15–36 |
| | | Mean tree diversity | No./plot | 3.06 \pm 1.23 | 1.26–5.23 |
| Mean tree basal area | | cm ² | 0.32 \pm 0.13 | 0.15–0.57 | |
| Mean tree density | | No./plot | 10.42 \pm 6.21 | 1.77–25.55 | |
| Proportion of non-native species | | Percent | 8.1 \pm 10.1 | 0–34 | |
| Total shrub diversity | | No. | 26.11 \pm 6.15 | 13–36 | |
| Mean shrub diversity | | No./plot | 2.29 \pm 0.65 | 1.40–3.70 | |
| Mean shrub basal area | | cm ² | 36.59 \pm 15.35 | 7.20–76.30 | |
| Mean herb diversity | | No./plot | 4.7 \pm 1.3 | 2.7–7.8 | |
| Landscape structure | Commercial/industrial/pavement | Percent | 5.20 \pm 8.07 | 0.10–33.29 | |
| | Commercial/residential | Percent | 19.50 \pm 20.21 | 0.30–71.65 | |
| | Rural residential | Percent | 2.57 \pm 1.54 | 0.40–5.12 | |
| | Turf | Percent | 17.32 \pm 4.86 | 0.48–49.15 | |
| | Turf and tree complex | Percent | 11.82 \pm 10.24 | 0.49–40.12 | |
| | Turf and grass | Percent | 1.76 \pm 2.51 | 0–8.71 | |
| | Pasture and hay and grass | Percent | 8.55 \pm 11.32 | 0.39–42.19 | |
| | Pasture and hay/exposed soil | Percent | 0.70 \pm 1.48 | 0–6.35 | |
| | Exposed soil/cropland | Percent | 1.22 \pm 1.73 | 0–7.26 | |
| | Exposed soil | Percent | 0.59 \pm 0.89 | 0–3.00 | |
| | Scrub and shrub | Percent | 0.57 \pm 0.74 | 0–2.47 | |
| | Deciduous forest | Percent | 41.56 \pm 29.53 | 0.92–85.06 | |
| | Deciduous forest and mtn. laurel | Percent | 0.89 \pm 1.12 | 0–4.00 | |
| | Coniferous forest | Percent | 3.65 \pm 3.77 | 0–15.11 | |
| | Forest/clear cut | Percent | 0.07 \pm 0.08 | 0–0.28 | |
| | Mixed forest | Percent | 0.13 \pm 0.25 | 0–0.84 | |
| | Deep water | Percent | 0.45 \pm 0.87 | 0–3.54 | |
| | Shallow water and mud flats | Percent | 0.21 \pm 0.47 | 0–1.90 | |
| | Non-forested wetland | Percent | 0.31 \pm 0.52 | 0–1.90 | |
| | Shrub wetland | Percent | 0.07 \pm 0.19 | 0–0.82 | |
| Deciduous forested wetland | Percent | 0.13 \pm 0.16 | 0–0.46 | | |
| Exposed ground and sand | Percent | 0.02 \pm 0.05 | 0–0.16 | | |

among each of three stream habitat units (pool, riffle, run) using standard methods (Barbour *et al.*, 1999; Lammert & Allan, 1999). To minimize the potential for community variation due to temporal effects, we sampled invertebrates within a limited time period (21 May to 9 June 1998). Sampling date was not correlated with the gradient in watershed household density. Habitat units were selected in randomized order beginning 25 m from the tributary's outlet and proceeding upstream to a predetermined 150 m maximum extent. Habitat units were assigned to collection sites based on localized stream flow, depth and channel morphology (Lamberti & Hauer, 1996). Samples were collected by positioning a 46-cm wide dipnet (500 micron mesh) immediately downstream of a 31 × 46 cm sampling quadrat ($A = 0.14 \text{ m}^2$) and by manually disturbing sediment for 2 min (Barbour *et al.*, 1999). If a sample included more than 100 individuals, the sample was homogenized on a number grid, and 100 organisms were selected by sequentially choosing random sections of the grid (Roy *et al.*, 2003; Weigel *et al.*, 2003). Organisms were identified to genus with standard literature (Peckarsky *et al.*, 1990; Merritt & Cummins, 1996; Wiggins, 1996). Taxon vouchers have been deposited at the Peabody Museum of Natural History at Yale University, New Haven, CT, USA.

Statistical analyses: multiscale environmental variation and communities

We focused our analysis on the composition and abundance of stream invertebrate communities. Multivariate redundancy analysis (hereafter, RDA) was used to evaluate relationships between stream invertebrate communities and environmental variation at each of four spatial scales. RDA is similar to multiple regressions, except that it allows for the analysis of multiple response variables. To remove collinearity among variables, a forward selection ($\alpha = 0.05$) procedure was applied in RDA to select and evaluate sets of environmental variables that each explained significant additional variation in stream community composition and abundance (ter Braak, 1996; ter Braak & Smilauer, 1998). Significance of canonical axes and variation explained by environmental variables were based on 10,000 Monte Carlo permutations. Preliminary analyses demonstrated that environmental variables explained the greatest variation in stream invertebrate communities at the scale of habitat units. Because we were interested in maximizing overall predictive success, subsequent analyses were conducted on the mean species abundances and habitat conditions of two replicates for each habitat type within a watershed. Performing analyses on individual sample data resulted in the same pattern of variation explained at different spatial scales as when samples were averaged. Partial RDA was used to estimate the contribution of local (habitat and reach) and landscape (riparian and watershed) scales to community variation after accounting for the other set of variables (ter Braak, 1996; Parris, 2004). In all analyses, proportions were angular-transformed, and macroinvertebrate abundances and human density were ln-transformed to correct for detected non-constant error variance.

Statistical analyses: spatial location and communities

We next evaluated the relationship between spatial location and community composition and abundance. Although a variety of statistical tests have been used to divide community variation into sources attributed to environmental variation and spatial autocorrelation (e.g. Mantel tests), canonical partitioning has emerged as the most powerful of available methods (Legendre *et al.*, in press). We assumed that positive spatial autocorrelation in community structure that is independent of variation explained by the environment provides an indication of community connectivity (Legendre & Legendre, 1998; Urban, 2004). We estimated the contribution of spatial processes to community structure through the use of stream reach coordinates associated with two dispersal models for aquatic organisms: (1) a random model that assumed equal rates of dispersal across both terrestrial and aquatic landscapes and (2) a network model that constrained movement to stream corridors (Macneale *et al.*, 2005). For the random dispersal model, we used Euclidean distances between sampling points, assuming that straight-line distances adequately reflected the probability of intercommunity dispersal. The geographical coordinates of the downstream sampling point of each tributary were expanded into third-order polynomial terms to allow for nonlinear responses (Legendre & Legendre, 1998). To evaluate proximity under the network dispersal model, we constructed a set of coordinates for each reach that described its location within the larger stream network based on the method of principal coordinates of neighbour matrices (PCNM) (Borcard & Legendre, 2002). PCNM provides a means to extract Euclidean coordinates from non-Euclidean distance matrices. To develop a relevant set of coordinates, we first calculated the distance between each sampling point and all others along the shortest river path by adding together intervening river segments in ARCVIEW version 3.3. In PCNM, a threshold distance is set such that both fine- and coarse-scale variations can be incorporated into a single analysis. We set our threshold distance to the maximum distance recorded within the river systems (51.6 km) because we assumed that aquatic dispersal between river systems would be limited given their outflows into a saltwater sound. In keeping with standard practice (Borcard & Legendre, 2002), we set all interstream system distances to four times this threshold value. The program DISTPCOA (<http://www.bio.umontreal.ca/casgrain/en/labo/distpcoa.html>) was then used to define sets of coordinate axes from this network distance matrix. We retained only coordinates associated with positive and non-zero eigenvalues for subsequent analyses. Each of the geographical and network coordinates was forward-selected in the same manner as environmental variables and then used to explain variation in community structure with RDA. Partial RDA also was used to estimate the contribution of spatial location to community variation after controlling for variation explained by watershed land use.

Statistical analyses: beta diversity

Decreasing connectivity among communities is expected to diminish the matching between specialist taxa and their dynamic

habitats (Chase & Leibold, 2002). We evaluated this prediction by examining the relationship between instream beta diversity and household density. Beta diversity was measured as one minus the mean of Jaccard's similarity index calculated among habitats (average of two replicates) within streams (Chase & Leibold, 2002). Three streams for which only one habitat type occurred in the specified study extent were excluded from this analysis.

RESULTS

Environmental variation and urbanization

We surveyed 18 streams and their surrounding watersheds along a rural–urban gradient that ranged from 0.2 to 38.4 households/ha (Fig. 1). In this region, 95% of anthropogenic land cover was devoted to residential, commercial and industrial uses. There was little agricultural land use. Anthropogenic land cover varied from 7 to 96% among watersheds. Human density was strongly and nonlinearly related to percentage anthropogenic land use (Fig. 2a; $P < 0.01$). Environmental variables collected at each spatial scale varied markedly among watersheds (see Table 1 for mean and range of all variables measured). Streams varied substantially in percentage clay/silt/sand substrate (range: 0–100%), nitrate concentration (10.8–113.4 μM), riparian tree density (2–26) and percentage watershed deciduous forest (1–85%).

Taxa diversity and urbanization

We identified *c.* 8600 stream invertebrates in 126 taxonomic groups. Of these groups, Diptera, Oligochaeta, Amphipoda, Trichoptera, Ephemeroptera, Coleoptera and Plecoptera were the most numerically dominant taxa (Appendix A). Mean invertebrate taxa richness ranged from 3.3 to 17.7 among streams. We found a strong negative correlation between human density and mean watershed taxa richness (Fig. 2b; OLS regression; $R^2 = 0.75$; $P < 0.0001$). This relationship remained significant even after the three most populated watersheds were removed from analysis ($P = 0.03$), suggesting that this pattern was robust to the influence of densely populated watersheds. This estimated relationship indicated that increases in watershed human density from 1 to 10 households per ha were accompanied by the loss of approximately half the species in local drainages. Ephemeroptera, Plecoptera and Trichoptera, taxa often associated with undisturbed streams (Barbour *et al.*, 1999), comprised 34% of invertebrate abundance sampled in less urbanized watersheds (< 1 household per ha) but only 11% of invertebrate abundance sampled in more urbanized watersheds (> 1 household per ha).

Multiscale environmental variation and communities

Despite the strong relationship between biodiversity and urbanization (Fig. 2b), local habitat conditions (including substrate, discharge and water chemistry) provided weak predictions of stream invertebrate community composition and abundance (Fig. 3). Habitat and stream reach variation only explained

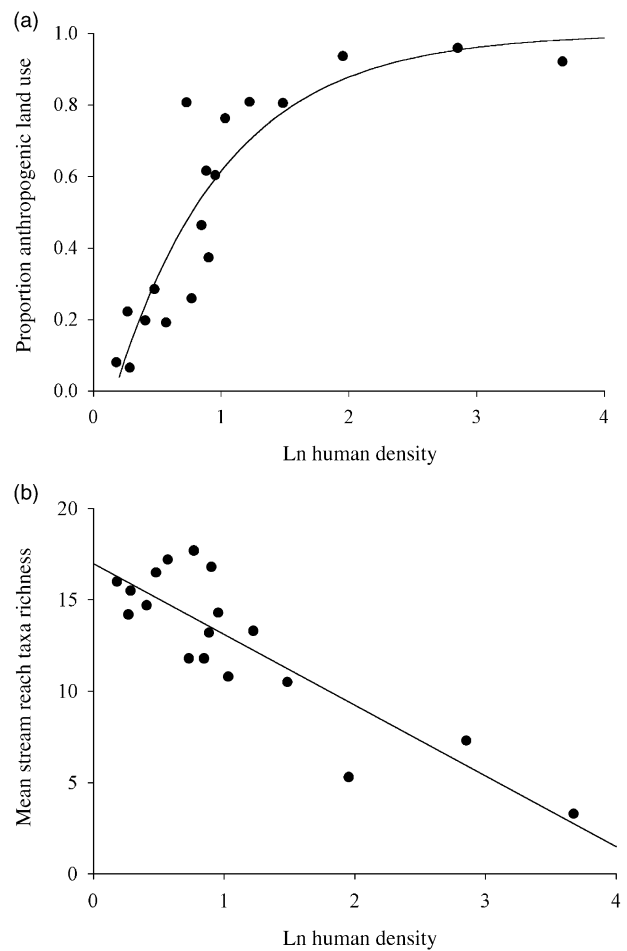


Figure 2 Relationships among invertebrate biodiversity, watershed land cover and household density. (a) Proportion of watershed area devoted to anthropogenic uses as a function of household density. Anthropogenic land use was defined as all categories identified by remote sensing for which active human disturbances can account for existing land cover. Model fit by nonlinear regression ($N = 18$; model: $y = 1 - 1.21\exp^{-1.15x}$; $P < 0.01$). (b) Mean stream reach taxa richness vs. household density. Reach taxa richness was calculated as the mean number of taxa identified from two replicate samples in each of three different habitat types (pools, runs, riffles). Model fit by OLS regression ($N = 18$, $R^2 = 0.75$, $P < 0.0001$).

6 and 16%, respectively, of community variation along the urbanization gradient. Instead, the strongest predictions of local stream invertebrate composition and abundance were based on variables collected at coarse scales. Variables describing riparian vegetation and landscape structure separately explained 30% of community structure (Fig. 3). For all analyses, relationships among canonical axes and community patterns were significant ($P < 0.005$). The best predictors of local stream invertebrate communities at these spatial scales (i.e. those retained in the RDA) were those variables that measured the extent of remnant vegetation (e.g. forest stand diversity and density; see Table 1). The percentage of remnant natural vegetation in a watershed explained a similar amount of variation in mean invertebrate taxa

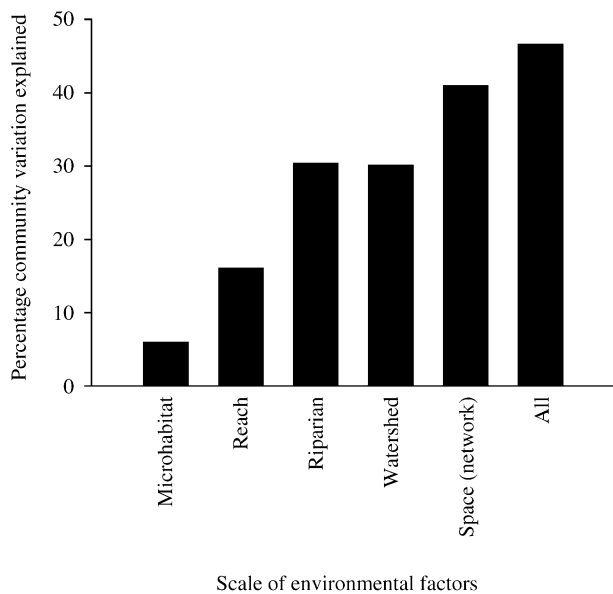


Figure 3 Percentage variation in community composition and abundance explained by selected environmental variables from each of four spatial classes, network spatial coordinates and all variables together. Redundancy analysis (RDA) was used to extract a subset of variables based on variance explained in stream invertebrate composition and abundance. Each non-redundant set of variables retained by RDA was significantly related to stream invertebrate community structure ($P < 0.005$).

richness ($R^2 = 0.70$; $P < 0.0001$) as population density ($R^2 = 0.75$). In the study region, less than 20% of forested land cover remained in watersheds with more than two households per ha.

We next used partial RDA to account for correlated effects among environmental variables collected at different spatial scales (ter Braak, 1996; Parris, 2004). Forward-selected factors from the riparian and watershed scales together explained 35% of the variation in community structure after removing variation explained by habitat and reach scales. In contrast, variables at local reach and habitat scales only explained 5% of community variation when the analysis was constrained by variables collected at riparian and watershed scales. These results suggested that riparian and watershed scales explained significant community structure independent of variation explained at reach and habitat scales.

Spatial location and communities

Six of the nine variables in the cubic polynomial spatial trend model were retained as significant and non-redundant spatial descriptors of stream invertebrate community variation. Geographical coordinates under the random dispersal model explained 21.2% of the variation in sampled communities. When this variation was constrained by variables selected in the watershed land use data set, a significant ($P = 0.0002$) portion of variation remained explained by spatial position (16.0%), which suggested that this effect was not due entirely to spatial autocorrelation in

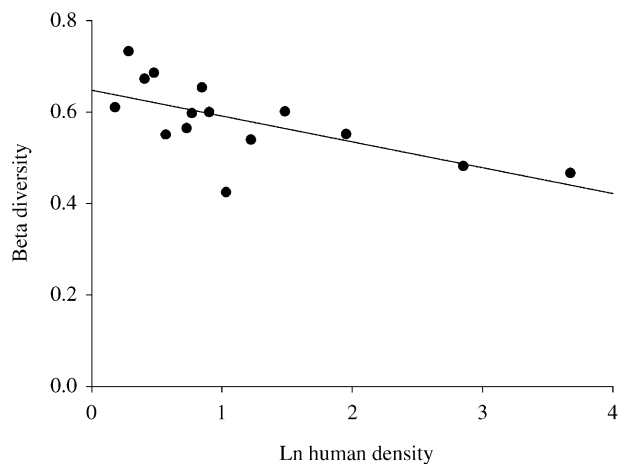


Figure 4 Relationship between among-habitat beta diversity and watershed household density. Beta diversity was measured as the average community dissimilarity (one minus Jaccard's index) among habitat units within each watershed. Line indicates OLS regression fit ($N = 15$; $R^2 = 0.43$; $P < 0.01$).

land use. In addition, geographical coordinates still explained 19.6% of variation after accounting for variation in stream reach altitude — an autocorrelated factor that often explains substantial coarse-scale variation in stream characteristics and communities (e.g. Townsend *et al.*, 2003).

Fourteen positive non-zero principal coordinate axes were extracted from the network distance matrix. Of these axes, 11 were retained following the RDA forward selection procedure ($\alpha = 0.05$). Network distance explained 41.0% of the variation in community composition and abundance — more than both the random dispersal model and any of the individual environmental data sets (Fig. 3). When the network distance data set was constrained by variables selected in the watershed variable data set in partial RDA, a substantial amount of variation was still explained by network coordinates (21.9%; $P = 0.0001$), even though about half the explanatory power was attributed to spatially autocorrelated changes in watershed land use. Constraining the network distance data set by altitude resulted in a reduction in variation explained of 3.3%, indicating that topography was not driving community spatial autocorrelation. Overall, a forward-selected model of environmental and network spatial variables collected from all scales explained 46.6% of stream invertebrate community structure (Fig. 3).

Beta diversity

Beta diversity, measured as among-habitat dissimilarity in community composition, varied as a negative function of watershed human density (Fig. 4; $N = 15$, $R^2 = 0.43$, $P < 0.01$). Communities were highly differentiated among local habitat types in rural watersheds and relatively similar in urbanized watersheds. Environmental variation among habitats within streams did not vary statistically across the urbanization gradient ($P = 0.94$), suggesting that this pattern was not due to the homogenization of habitat differences in urban streams.

DISCUSSION

Previous research has established that local instream conditions (Roy *et al.*, 2003; Wang *et al.*, 2003; Heino *et al.*, 2004) and the effect of watershed land use on instream physical and chemical processes (Richards *et al.*, 1996; Allan *et al.*, 1997; Lammert & Allan, 1999; Wang *et al.*, 2001; Snyder *et al.*, 2003; Weigel *et al.*, 2003; King *et al.*, 2005) can predict variation in stream invertebrate communities. Among the four scales of environmental variation analysed in our study, riparian and watershed land cover explained more variation than that explained by instream physical and chemical properties. Spatial coordinates that take into account network distance among stream reaches were better predictors of community composition and abundance than geographical coordinates as well as any of the environmental data sets. These results contribute to our ability to predict stream communities in three ways. First, we provide corroborating evidence that remnant natural vegetation along riparian corridors and within watersheds is an important predictor of stream invertebrate communities along rural–urban gradients (e.g. King *et al.*, 2005; Moore & Palmer, 2005). Second, we show the usefulness of PCNM for extracting relevant spatial coordinates from stream network distances. Third, our results suggest that a patch dynamics perspective that takes into account network distance among stream reaches can generate accurate predictions of stream invertebrate communities along urbanization gradients.

Results suggested that remnant vegetation cover over coarse spatial extents (riparian and watershed scales) provided better predictions of local stream biodiversity than local instream physical and chemical conditions in our system. Remnant forest cover, by itself, explained 70% of the variation in watershed invertebrate richness. Likewise, another study of urban headwater streams found that riparian forest cover explained 75% of the variation in invertebrate species richness (Moore & Palmer, 2005). Together, these results suggest that urbanization often may shape local stream biodiversity by limiting remnant native vegetation cover over coarser spatial extents (i.e. the riparian and watershed scales). In this way, maintaining or restoring riparian vegetation may provide a buffer against moderate watershed urbanization (Paul & Meyer, 2001; Wang *et al.*, 2001; Allan, 2004; Moore & Palmer, 2005).

The significant predictions provided by coarse-scale riparian and watershed environmental variation might be explained by several factors. First, the intense disturbance gradient (range: 0.2–38.4 households per ha) that characterized our study region likely influenced the relative importance of variables collected at coarse scales. Regional mechanisms may become more important for predicting stream invertebrate communities when coarse-scale anthropogenic disturbances overshadow the importance of local habitat variation (Wang *et al.*, 2003; Allan, 2004). This finding suggests that restoration of urban streams often will require a coarse landscape perspective that matches the scale of anthropogenic disturbances. Second, we cannot exclude the possibility that unmeasured environmental variation affected predictions. However, we included a relatively large number of

environmental variables that were suggested by prior literature to drive variation in stream invertebrate communities. Third, factors at local scales may have been correlated with riparian and watershed variables and thus could have contributed to the success of predictions made at coarser scales. Although correlations certainly existed between variables collected at different spatial scales, predictions made by regional (riparian and watershed) variables were substantially independent of predictions generated by local habitat and reach variation after statistically controlling for these effects in partial RDA. This result indicates the potential operation of different mechanisms at divergent scales. Fourth, because environmental variables were indicative of a variety of potential mechanisms that shape communities, conclusions may have differed if a single variable had been measured across all scales. Based on the importance of remnant vegetation in our analyses, we encourage future efforts to focus on measuring vegetation characteristics across multiple scales. Lastly, all conclusions should be interpreted with caution since they are based on field observations that cannot be used to infer causation.

Our results indicated the importance of a network approach to understanding spatial autocorrelation in stream communities. Stream community studies that have incorporated spatial autocorrelation have generally relied on Euclidean distance among reaches (e.g. Townsend *et al.*, 2003; Wang *et al.*, 2003; King *et al.*, 2005) rather than on stream network distance (Fagan, 2002). However, in our study, network position explained more variation (41%) in community structure than standard geographical position (21%) or any of the sets of environmental variables (6–30%). Stream invertebrates most frequently disperse within a corridor of a few hundred metres or less from the streambed (Petersen *et al.*, 2004; Macneale *et al.*, 2005), possibly explaining the stronger support for the network over the random dispersal model. Both geographical and network coordinates were significant predictors of community structure even after controlling for potential autocorrelation of watershed land use. We cannot rule out the influence of unmeasured basin-scale environmental variables on community autocorrelation. However, community spatial structure was independent of altitude, and all streams shared the same glacial alluvial surficial material — two factors commonly cited as contributing to among-watershed invertebrate community variation (Wang *et al.*, 2003).

If interreach connectance was an important driver of community assembly, we might expect that the sorting of specialists among habitat units would be affected by landscape constraints on dispersal. In agreement with this prediction, we found that community differentiation among habitat units varied depending on watershed urbanization. Species inhabiting urbanized streams were distributed uniformly across habitat types, whereas species in rural streams were highly differentiated among local habitats. Extreme disturbance events associated watershed land use alterations such as flash floods could eliminate habitat specialists by homogenizing instream habitat variation (Allan, 2004). However, in this study, urbanization was not associated with a decrease in the variation among habitat substrate and flow characteristics. Instead, observed variation in beta diversity along

the urbanization gradient may be explained either by the selective extinction of habitat specialists in urbanized streams or by a process through which habitat-specific taxa disproportionately fail to disperse across urbanized landscapes. These two processes, selective extinction and dispersal limitation, may act together to generate and reinforce changes in community structure due to urbanization (Bohonak & Jenkins, 2003; Townsend *et al.*, 2003; Petersen *et al.*, 2004).

Dispersal limitation may be an important, albeit frequently overlooked, determinant of community composition along urbanization gradients. Many of the insect orders found exclusively in less urbanized watersheds in this study (e.g. Plecoptera) are known to be restricted in their movement across non-forested land cover (Petersen *et al.*, 1999). Limited dispersal rates are expected to drive community dynamics in streams that undergo more frequent or severe disturbances (Palmer *et al.*, 1996). Hence, urbanization may alter local colonization–extinction dynamics both by increasing the severity of disturbances and by restricting dispersal that would otherwise provide for the recolonization of locally extirpated species. By restricting dispersal, landscapes modified by humans may act as a primary filter on stream biodiversity (*sensu* Poff & Huryn, 1997).

Our results suggested that protecting or restoring terrestrial movement corridors along and between stream reaches could aid the conservation of invertebrate communities in urbanizing watersheds. Providing these corridors of remnant habitat has not been an explicit focus of the majority of stream restoration activities (Bernhardt *et al.*, 2005). Yet, a growing body of literature recommends the restoration of natural dispersal routes to conserve aquatic biodiversity (Wishart & Davies, 2003; Briers & Gee, 2004; Petersen *et al.*, 2004). We hope that this research will encourage a patch-dynamics perspective in future stream conservation and restoration. To promote the dispersal function of landscapes, riparian vegetation should be maintained and restored in continuous tracts through as much of the stream system as practical. In addition, our findings suggest that the maintenance or creation of undisturbed landscape corridors among watersheds can facilitate long-distance dispersal among stream systems.

CONCLUSIONS

Projected increases in global urbanization (UN Human Settlements Programme, 2004) have the potential to significantly reduce global biodiversity during the 21st century. Stream biodiversity is at particular risk because of its sensitivity to anthropogenic disturbances and because urbanization frequently occurs along rivers (Malmqvist & Rundle, 2002). The restoration of aquatic biodiversity is often attempted by returning local within-stream habitat to undisturbed conditions (Bernhardt *et al.*, 2005). However, our findings suggest that urbanization can cause loss of stream invertebrate diversity at spatial scales well beyond instream habitats. If landscape fragmentation frequently limits the movement of species in urban ecosystems, then the restoration of natural landscape corridors within and between watersheds will be important for preserving stream biodiversity in an urbanizing world.

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Appendix A List of taxonomic groups collected from 18 headwater streams in New Haven County, Connecticut, USA in summer 1998. Stream distribution indicates the number of streams from which a particular taxon was collected

| Higher taxa | Order | Family | Genus | Total individuals | Stream distrib. |
|-------------|---------------|-----------------|-----------------------|-------------------|-----------------|
| Insecta | Coleoptera | Chrysomelidae | <i>Hydrothassa</i> | 1 | 1 |
| | Coleoptera | Curculionidae | <i>Stenopelmus</i> | 4 | 1 |
| | Coleoptera | Curculionidae | Sp. a | 2 | 4 |
| | Coleoptera | Dytiscidae | <i>Agabus</i> | 8 | 6 |
| | Coleoptera | Dytiscidae | <i>Potamonectes</i> | 1 | 1 |
| | Coleoptera | Elmidae | <i>Dubiraphia</i> | 36 | 10 |
| | Coleoptera | Elmidae | <i>Gonielmis</i> | 13 | 6 |
| | Coleoptera | Elmidae | <i>Macronychus</i> | 4 | 5 |
| | Coleoptera | Elmidae | <i>Microcylloepus</i> | 3 | 2 |
| | Coleoptera | Elmidae | <i>Optioservus</i> | 76 | 9 |
| | Coleoptera | Elmidae | <i>Oulimnius</i> | 44 | 8 |
| | Coleoptera | Elmidae | <i>Promoresia</i> | 23 | 5 |
| | Coleoptera | Elmidae | <i>Stenelmis</i> | 324 | 13 |
| | Coleoptera | Haliplidae | <i>Haliplus</i> | 1 | 1 |
| | Coleoptera | Haliplidae | <i>Pelodytes</i> | 18 | 3 |
| | Coleoptera | Hydraenidae | <i>Hydraena</i> | 2 | 2 |
| | Coleoptera | Psephenidae | <i>Ectopria</i> | 15 | 8 |
| | Coleoptera | Psephenidae | <i>Psephenus</i> | 18 | 7 |
| | Coleoptera | Ptilodactylidae | <i>Anchytarsus</i> | 2 | 1 |
| | Coleoptera | Tenebrionidae | <i>unknown</i> | 1 | 1 |
| | Collembola | Entomobryidae | <i>Cyphoderus</i> | 1 | 1 |
| | Collembola | Isotomidae | <i>Stachanorema</i> | 2 | 1 |
| | Collembola | Isotomidae | Sp. a | 1 | 1 |
| | Collembola | Isotomidae | Sp. b | 1 | 1 |
| | Collembola | Sminthuridae | <i>Bourletiella</i> | 1 | 1 |
| | Diptera | Ceratopogonidae | <i>Atrichopogon</i> | 1 | 1 |
| | Diptera | Ceratopogonidae | Sp. a | 8 | 8 |
| | Diptera | Chironomidae | | 3725 | 18 |
| | Diptera | Empididae | <i>Chelifera</i> | 6 | 5 |
| | Diptera | Empididae | <i>Hemerodromia</i> | 22 | 8 |
| | Diptera | Simuliidae | | 112 | 11 |
| | Diptera | Stratiomyidae | <i>Nemotelus</i> | 2 | 3 |
| | Diptera | Stratiomyidae | Sp. a | 1 | 1 |
| | Diptera | Tabanidae | <i>Tabanus</i> | 4 | 1 |
| | Diptera | Tipulidae | <i>Antocha</i> | 95 | 10 |
| | Diptera | Tipulidae | <i>Cryptolabis</i> | 1 | 1 |
| | Diptera | Tipulidae | <i>Dicranota</i> | 34 | 7 |
| | Diptera | Tipulidae | <i>Hexatoma</i> | 10 | 2 |
| | Diptera | Tipulidae | <i>Limonia</i> | 1 | 1 |
| | Diptera | Tipulidae | <i>Pedicia</i> | 1 | 1 |
| | Diptera | Tipulidae | <i>Tipula</i> | 11 | 9 |
| | Ephemeroptera | Baetidae | <i>Acentrella</i> | 1 | 1 |
| | Ephemeroptera | Baetidae | <i>Barbaetis</i> | 14 | 2 |
| | Ephemeroptera | Baetidae | <i>Baetis</i> | 498 | 13 |
| | Ephemeroptera | Caenidae | <i>Caenis</i> | 2 | 2 |
| | Ephemeroptera | Ephemerellidae | <i>Attenella</i> | 8 | 4 |
| | Ephemeroptera | Ephemerellidae | <i>Dannella</i> | 4 | 3 |
| | Ephemeroptera | Ephemerellidae | <i>Drunella</i> | 3 | 2 |
| | Ephemeroptera | Ephemerellidae | <i>Ephemerella</i> | 98 | 5 |
| | Ephemeroptera | Ephemerellidae | <i>Eurylophella</i> | 20 | 6 |
| | Ephemeroptera | Ephemerellidae | <i>Serratella</i> | 5 | 5 |
| | Ephemeroptera | Ephemerellidae | <i>Timpanoga</i> | 2 | 1 |
| | Ephemeroptera | Ephemerellidae | Sp. a | 3 | 3 |
| | Ephemeroptera | Heptageniidae | <i>Epeorus</i> | 1 | 1 |
| | Ephemeroptera | Heptageniidae | <i>Nixe</i> | 6 | 1 |

Appendix A Continued

| Higher taxa | Order | Family | Genus | Total individuals | Stream distrib. |
|-------------|---------------|-------------------|---------------------------|-------------------|-----------------|
| | Ephemeroptera | Heptageniidae | <i>Stenonema</i> | 28 | 5 |
| | Ephemeroptera | Heptageniidae | Sp. a | 4 | 5 |
| | Ephemeroptera | Leptophlebiidae | | 13 | 4 |
| | Ephemeroptera | Ameletidae | <i>Ameletus</i> | 1 | 1 |
| | Ephemeroptera | Tricorythidae | <i>Tricorythodes</i> | 4 | 1 |
| | Hemiptera | Corixidae | <i>Hesperocorixa</i> | 1 | 1 |
| | Hemiptera | Corixidae | Sp. a | 3 | 3 |
| | Hemiptera | Gerridae | <i>Gerris</i> | 1 | 1 |
| | Hemiptera | Hebridae | <i>Hebrus</i> | 2 | 1 |
| | Hemiptera | Mesoveliidae | <i>Mesovelia</i> | 2 | 2 |
| | Hemiptera | Veliidae | <i>Rhagovelia</i> | 7 | 3 |
| | Lepidoptera | Noctuidae | | 1 | 1 |
| | Megaloptera | Corydalidae | <i>Nigronia</i> | 43 | 7 |
| | Megaloptera | Sialidae | <i>Sialis</i> | 1 | 1 |
| | Odonata | Calopterygidae | <i>Calopteryx</i> | 3 | 2 |
| | Odonata | Calopterygidae | Sp. a | 1 | 1 |
| | Odonata | Coenagrionidae | <i>Argia</i> | 1 | 1 |
| | Odonata | Coenagrionidae | <i>Amphiagrion</i> | 2 | 2 |
| | Odonata | Coenagrionidae | Sp. a | 3 | 2 |
| | Odonata | Cordulegastridae | <i>Cordulegaster</i> | 4 | 2 |
| | Odonata | Gomphidae | <i>Dromogomphus</i> | 4 | 1 |
| | Odonata | Gomphidae | <i>Lanthus</i> | 29 | 7 |
| | Odonata | Gomphidae | <i>Stylogomphus</i> | 9 | 4 |
| | Plecoptera | Chloroperlidae | <i>Alloperla/Suwallia</i> | 8 | 4 |
| | Plecoptera | Leuctridae | <i>Leuctra</i> | 194 | 8 |
| | Plecoptera | Nemouridae | <i>Amphinemura</i> | 5 | 3 |
| | Plecoptera | Nemouridae | Sp. a | 3 | 3 |
| | Plecoptera | Peltoperlidae | <i>Tallaperla</i> | 8 | 2 |
| | Plecoptera | Peltoperlidae | Sp. a | 48 | 3 |
| | Plecoptera | Perlidae | <i>Eccopectura</i> | 2 | 1 |
| | Plecoptera | Perlidae | <i>Perlesta</i> | 4 | 2 |
| | Plecoptera | Perlidae | Sp. a | 1 | 1 |
| | Plecoptera | Perlodidae | <i>Isoperla</i> | 9 | 3 |
| | Plecoptera | Pteronarcyidae | <i>Pteronarcys</i> | 1 | 1 |
| | Plecoptera | Taeniopterygidae | <i>Taeniopteryx</i> | 8 | 4 |
| | Trichoptera | Apataniidae | <i>Apatania</i> | 4 | 1 |
| | Trichoptera | Brachycentridae | <i>Micrasema</i> | 5 | 2 |
| | Trichoptera | Glossosomatidae | <i>Agapetus</i> | 2 | 2 |
| | Trichoptera | Glossosomatidae | <i>Glossosoma</i> | 72 | 9 |
| | Trichoptera | Hydropsychidae | <i>Hydropsyche</i> | 164 | 14 |
| | Trichoptera | Hydropsychidae | <i>Cheumatopsyche</i> | 71 | 7 |
| | Trichoptera | Hydropsychidae | <i>Diplectronea</i> | 1 | 1 |
| | Trichoptera | Hydroptilidae | <i>Hydroptila</i> | 15 | 5 |
| | Trichoptera | Hydroptilidae | <i>Orthotrichia</i> | 1 | 1 |
| | Trichoptera | Lepidostomatidae | <i>Lepidostoma</i> | 11 | 4 |
| | Trichoptera | Leptoceridae | <i>Mystacides</i> | 11 | 1 |
| | Trichoptera | Leptoceridae | <i>Oecetis</i> | 1 | 2 |
| | Trichoptera | Limnephilidae | <i>Hydatophylax</i> | 10 | 5 |
| | Trichoptera | Limnephilidae | <i>Ironoquia</i> | 1 | 1 |
| | Trichoptera | Limnephilidae | <i>Psychoglypha</i> | 3 | 1 |
| | Trichoptera | Limnephilidae | Sp. a | 23 | 2 |
| | Trichoptera | Philopotamidae | <i>Dolophilodes</i> | 76 | 9 |
| | Trichoptera | Polycentropodidae | <i>Nyctiophylax</i> | 9 | 3 |
| | Trichoptera | Polycentropodidae | <i>Polycentropus</i> | 8 | 3 |
| | Trichoptera | Psychomiidae | <i>Lype</i> | 1 | 1 |
| | Trichoptera | Rhyacophilidae | <i>Rhyacophila</i> | 21 | 4 |

Appendix A Continued

| Higher taxa | Order | Family | Genus | Total individuals | Stream distrib. |
|--------------|-------------|----------|------------------|-------------------|-----------------|
| | Trichoptera | Uenoidae | <i>Neophylax</i> | 115 | 6 |
| | Amphipoda | | | 573 | 14 |
| | Decapoda | | | 5 | 3 |
| | Isopoda | | | 150 | 12 |
| Arachnidia | | | | 4 | 2 |
| Hirudinea | | | | 4 | 2 |
| Hydrachnidia | | | | 6 | 3 |
| Gastropoda | | | | 127 | 13 |
| Bivalvia | | | | 71 | 10 |
| Nematoda | | | | 4 | 1 |
| Oligochaeta | | | | 1234 | 18 |
| Turbellaria | | | | 1 | 1 |