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Stream fish community structure across an urban gradient in a northeastern US watershed

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Abstract Anthropogenic land cover change in watersheds has the potential to degrade stream habitat quality and alter fish assemblage structure. The objective of this study was to examine the relative importance of urbanization at different spatial scales and local habitat conditions on both the fish taxonomic assemblage and trait assemblage. Fish assemblages were sampled in 22 wadeable streams within a single sub-basin in the northeastern USA. Urbanized land cover at the watershed and riparian scales was associated with increases in specific conductivity and pH, but was not a major determinant of taxonomic or trait assemblage structure. Instead, taxonomic and trait assemblages were associated with a gradient of decreasing elevation and increasing temperature, and some of the most urbanized sites supported diverse and unique fish assemblages. These results contribute to a greater understanding of the variation in the effects of urbanization on stream health.

Keywords Fish assemblage · Species traits · Variation partitioning · Local contribution to biotic diversity · Urbanization

Introduction

Understanding the factors that drive patterns of species distributions is fundamental to a better understanding of an ecosystem. This has been a central focus of the field of community ecology, illuminating our understanding of how the natural world is formed and sustained as well as providing guidance for human land cover and habitat conservation and management. Despite concerted efforts in understanding the patterns and processes involved in the distribution of organisms and the factors responsible for these distributions, a review by Siqueira et al. (2015) found that more focus has been on terrestrial systems and called for a greater focus on aquatic ecosystems.

One important driver of species patterns is the effect of human activities on habitats and ecosystems. Streams and stream fish assemblages in the northeastern USA have experienced a long legacy of anthropogenic impacts (Foster 2002). Changes to the surrounding vegetation (agriculture, deforestation, and reforestation) and

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increased industrial and residential development have affected streams. Dams have altered the natural flow regime (Poff et al. 1997), and non-indigenous fish species have been widely introduced. Increased developed land cover is associated with more impervious surfaces (e.g., pavement) that shed precipitation directly into waterways rather than allowing infiltration (Booth 1991; see also review by Shuster et al. 2005). Increased watershed impervious surface area may lead to elevated stream temperatures (Nelson and Palmer 2007; Somers et al. 2013; Hassett et al. 2018), altered hydrology (Brown et al. 2009), and increases in conductivity (Soper et al. 2021). Urbanized streams often have elevated specific conductivity from winter deicers used on roadways (Kaushal et al. 2018) and increased nutrients, pesticides, herbicides, and pharmaceuticals from lawns and sewage effluent (Brown et al. 2009). Altered urban stream conditions can result in decreased fish and macroinvertebrate diversity and abundance (Moore and Palmer 2005; Morgan and Cushman 2005). Meyer et al. (2005) designated these seemingly consistent responses of stream ecosystem degradation in urban areas the "urban stream syndrome." However, subsequent research has demonstrated significant variation in the response of stream health to urbanization (Meyer et al. 2005; Shuster et al. 2005; Booth et al. 2016).

The response of stream fish assemblages to urban land cover may depend on spatial scale (Allan et al. 1997; Lammert and Allan 1999; Wang et al. 2003; Cervantes-Yoshida et al. 2015). Watershed scale variables like the percentage of impervious cover are frequently used to quantify the impact of developed land cover for specific study sites (Alford and Jackson 2010; Angermeier and Winston 1998; Brazner et al. 2005; Wang et al. 2006; Marzin et al. 2013). However, by influencing local habitat conditions, riparian land cover may have greater relevance to fish assemblages than watershed-scale metrics (Wang et al. 2001; Brazner et al. 2005; Cervantes-Yoshida et al. 2015). At the smallest spatial scale, reach-scale habitat conditions affect fish assemblages (e.g., Alford 2014; Angermeier and Winston 1998; Czeglédi et al. 2020). For example, stream width, stream depth, gradient, elevation, water temperature, and the pool/riffle ratio differed among five

stream fish assemblage types in CT, USA (Kanno and Vokoun 2008). Substrate composition has been shown to help predict the abundance (Mesquita et al. 2006) and composition (Mullen et al. 2011) of stream fish assemblages. Stream temperature in particular has long been recognized as an important constraint on the distribution of many fishes (Beauchene et al. 2014).

Researchers have used a variety of approaches to quantify fish diversity when studying urban impacts. Both the number and relative abundance of species (alpha diversity) have long been used to characterize community structure, but there is a growing emphasis on trait diversity in communities (Winemiller 2005; Frimpong and Angermeier 2009, 2010). Fish traits have been combined with information on species composition in biological metrics used to assess habitat quality (e.g., Index of Biotic Integrity, Karr 1981). Fish traits include biological (e.g., growth, reproduction) and ecological (habitat, diet) characteristics, and traits can provide important information about community function (Poff 1997; Olden et al. 2010; Pool et al. 2010; Pease et al. 2012). The relative importance of associations between species or trait assemblages and stream habitat and land cover variables can be assessed with multivariate analyses and variation partitioning (e.g., Maasri et al. 2019). Beta diversity is the variation in species composition among sites within a particular geographical area (Whittaker 1960). Local contribution to beta diversity (LCBD; Legendre and De Cáceres 2013) is a relatively new metric quantifying the contribution of a site to overall regional diversity and highlighting sites that possess unique community composition.

The objective of this study was to examine the relative importance of urbanization at different spatial scales and local habitat conditions on both fish taxonomic assemblage and trait assemblage using variation partitioning. Landscape metrics of urbanization were calculated for the entire watershed upstream of sites, for the watershed riparian zone, and the riparian zone of each sampled stream reach in a single sub-basin of the Nashua River in central Massachusetts. We also included local physical conditions relevant to fish in our models. We expected that fish taxonomic and trait assemblages would be most sensitive to urbanization impacts in the watershed riparian zone and in the riparian zone of the sampled reach.

## Materials and methods

Study area and sampling sites

The study area was a single sub-basin (Nashua River HUC 8-01070004) in the Gulf of Maine Coastal Plain ecoregion of the Northeastern Coastal Plain (Fig. 1). As of 2016, forest constituted 59.2% of sub-basin land area and developed land constituted 18.6% (NLCD 2016). Sampling sites on unique tributaries of the Nashua River were chosen to cover a broad range of urban land cover and were selected based on available access, likely perennial streamflow, the presence of hard-bottom riffle habitats in at least part of the reach, and drainage area greater than or equal to 1 km^2 (see Table 1 for names of sites). Following Shank et al. (2016), the length of each reach was equal to 10 times the mean wetted width (determined over equally spaced transects), with a minimum reach length of 100 m. Sampling reaches were typically 100-m long, and GPS coordinates of the upstream and downstream ends of the reach were recorded.

Fish sampling

Fish were collected by backpack electroshocking (Smith-Root Model LR-24) by teams of three or more people (one person using the electroshocker and a minimum of two others using dip nets to collect the fish). Nine sites were sampled in 2018, eleven sites in 2019, and five sites in 2020 (all collected during June and July). Each site had block nets set up at the upstream and downstream ends of the reach to prevent fish from escaping. As most streams were wide enough to prevent the entire stream from being sampled at once (Table 1), a two-pass electrofishing procedure was performed at each site (Shank et al. 2016). One-half of the stream was arbitrarily selected, and fish were collected from that side, going from downstream to upstream. This was then repeated on the other half of the stream that was not sampled the first time. After both sides were done, all fish were identified in the field and measured for total length. When necessary, fish were preserved and returned to the lab for identification. Fish with a total length of < 40 mm were removed from the dataset because electroshocking is less effective for smaller fish (Armstrong et al. 2011). Additionally, brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*) were removed from the dataset if the total length was > 200 mm because of widespread recreational stocking (Armstrong et al. 2011). Thirty-eight species traits were obtained from Frimpong and Angermeier (2009), covering essential

Fig. 1 Nashua River sub-basin with the 22 study watersheds outlined. Filled black circles indicate sampling locations. The river mainstem flows towards the northeast within the basin
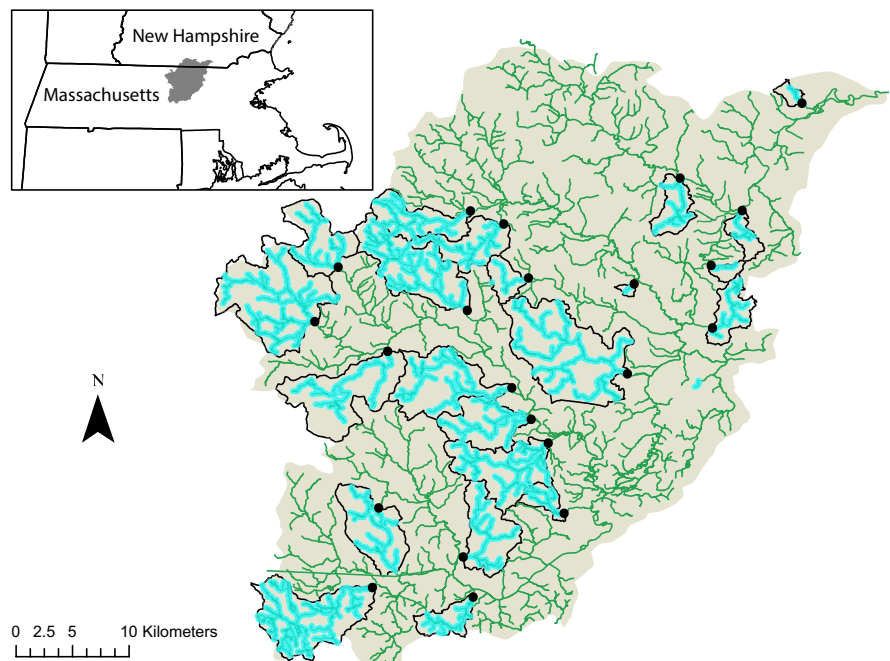
Table 1 Physical and land use characteristics of study streams

Name	Stream width (m)	Elevation (m)	Median substrate size (mm)	Canopy openness (%)	Discharge (m³ s⁻¹)	Average of daily mean temperature (°C)	Maximum 15 minute change in temperature (°C)	Watershed developed land use (%)	Watershed pasture, hay, and crop land use (%)	Watershed forest land use (%)
Asnebumskit Brook (Asneb)	7.9	191	30	18.1	0.58	20.2	0.4	18	7	56
Unnamed Brook at Broad Hill (Broad)	2.0	55	37	1	0.04	20.0	3.7	63	9	22
Catacoonamug Brook (Catac)	7.7	74	50	17.2	9.1	24.0	1.2	21	7	47
Fall Brook (Fall)	4.0	83	2	36.5	0.82	19.2	2.1	49	4	36
Falulah Brook (Falul)	5.2	122	87	55	1.19	22.9	1.5	11	5	75
Flag Brook (Flag)	6.2	181	69.5	6.6	0.79	24.2	1.1	13	2	67
Gates Brook (Gates)	3.6	127	35	7.2	0.87	16.5	3.1	58	5	28
Goodridge Brook (Goodr)	2.1	104	40	6.9	0.18	22.1	0.3	40	19	26
James Brook (James)	5.2	66	23	12.2	0.64	22.1	1.2	25	14	36
Monoosnoc Brook (Monoo)	5.3	91	77	61.9	0.49	20.9	4.3	25	1	64
Mulpus Brook (Mulpu)	3.3	127	60	4.3	0.15	19.3	0.6	9	8	70
Nod Brook (Nod)	2.3	61	11	4.3	0.01	17.5	2.7	18	13	52
Pearl Hill Brook (Pearl)	5.5	112	14	8.5	0.19	21.0	0.3	5	1	85
Phillips Brook (Phill)	4.2	259	57	29.7	0.11	22.2	0.9	8	3	74
Reedy Meadow Brook (Reedy)	3.0	53	2	2.7	0.16	23.0	2.0	21	7	46
Sucker Brook (Sucke)	5.1	63	2	26.9	0.31	21.6	0.3	13	12	60
Trap Swamp Brook (Trap)	2.1	79	21	7.4	0.07	20.6	1.5	9	0	80
Trout Brook (Trout)	5.3	166	44	5.4	0.5	20.5	0.4	5	5	74
Waushacum Brook (Waush)	4.7	125	64.5	4.3	1.45	23.7	0.8	17	5	55

Table 1 (continued)

Name	Stream width (m)	Elevation (m)	Median substrate size (mm)	Canopy openness (%)	Discharge (m³ s⁻¹)	Average of daily mean temperature (°C)	Maximum 15 minute change in temperature (°C)	Watershed developed land use (%)	Watershed pasture, hay, and crop land use (%)	Watershed forest land use (%)
Wekepeke Brook (Wekep)	4.5	83	27.5	35.8	0.01	16.3	3.2	17	9	58
Whitman River (Whitm)	6.6	238	70	3.8	4.63	22.2	0.8	9	4	70
Willard Brook (Willa)	6.4	132	53	10.6	0.17	20.5	0.5	8	4	80
Average	4.6	118	39.8	16.7	1.0	20.9	1.5	21	7	57

biological and ecological characteristics like reproduction, habitat, diet, and body size. Traits characterized by continuous data were transformed into categorical values (see Supplemental Table 1S for more details).

Field measurements

Field measurements were recorded at the same stream reach and typically in the same season as fish collections. The median substrate size in each reach was measured using a Wolman pebble count (mean counted = 105 particles, min = 60, Wolman 1954). Canopy openness was measured with a spherical densiometer near the center of the channel at five randomly selected locations within stream riffles. Discharge was measured during the summer baseflow season by determining the cross-sectional area of the stream and measuring water velocity with a Global Water velocity meter (Flow Probe 211). One water sample (approximately 2100 mL) per stream was collected in the field, transported to the lab on ice, and analyzed the same day in the laboratory using colorimetric methods on a Hach DR 3900 spectrophotometer for total phosphorus (2742745), reactive phosphate (2742545), nitrate (TNT 835), nitrite (TNT 839), and ammonia (TNT 830). Handheld water quality meters were used on-site to record dissolved oxygen (YSI ProODO), specific conductivity (YSI Pro 30), turbidity (Oakton Turbidimeter T-100), and pH (YSI Pro 10) once per stream. One temperature logger (HOBO® Pendant UA-002-08, Onset Computer Corporation, Bourne, MA, USA) was deployed at each of the stream sites in summer 2020 (June 21–July 16, 2020) and recorded stream temperature every 15 min for the entire duration of their deployment. Ice-bath calibration showed that all loggers were recording within manufacturer tolerances (± 0.53 °C) before deployment. Of the initial 25 sites, the loggers at two were lost, and one site dried up during the study, so these were excluded from all analyses, resulting in a total of 22 stream sites.

Geospatial analyses

Land cover was characterized using a Geographical Information System in ArcGIS Pro 2.6.0 (Esri Inc., 2020). Land cover was characterized and analyzed at multiple spatial scales (see Wang et al. 2001; Rowe et al. 2009; Stephenson and Morin 2009). In our

study, three nested spatial scales (watershed (SW), riparian (SR), and reach (R)) were used. Watersheds were delineated in StreamStats (Version 4, U.S. Geological Survey) based on the downstream end of the sampling reach. Riparian land cover in the watershed was characterized by a 50-m buffer on either side of all stream lines, and reach land cover was characterized by the same 50-m buffer for the sampled stream reach. Fifty meters was chosen because this was the smallest extent that land cover could be measured by remote sensing techniques. We included metrics of anthropogenic land cover from Falcone et al. (2010) that were relevant at the watershed, riparian, and reach spatial scales. Housing density (HUDEN) and road density (ROADDEN) were calculated from 2010 US Census Bureau data. Percent developed (DEV) and combined percent pasture, hay, and crop (PastureHayCrops) land cover were calculated from the 2016 National Land Cover Dataset. Stream slope was calculated from Model My Watershed (Stroud Water Research Center, http://www.stroudcenter.org), and elevation was obtained from the National Map (US Geological Survey).

Statistical analyses

Environmental conditions and response variables

The average of mean daily stream temperature (ADMeanT) and the coefficient of variation of daily mean temperature (CVDMeanT) were calculated for each stream. We also calculated the maximum change in temperature between 15 min measurements for each stream (MaxCT) to examine the impact of increased impervious surface area on summer storm runoff (Hassett et al. 2018). Predictor variables were log (elevation, openness, specific conductivity, HUDEN_SW, ROADDEN_SW, Dev_SW, HUDEN_SR, ROADDEN_SR, Dev_SR) or log+1 (discharge, ammonia, MaxCT, PastureHayCrops_SW, PastureHayCrops_SR, HUDEN_R, ROADDEN_R, Dev_R) transformed as necessary for subsequent analyses. Associations among fish habitat variables (see *Univariate variation partitioning* below) and land cover at the three spatial scales were examined using Spearman's rank correlations, and *p*-values were corrected for multiple testing using the false discovery rate technique (Benjamini and Hochberg 1995). To account for low detection probabilities of rare

species, we calculated total species richness at each site using the improved Chao non-parametric species richness estimator for abundance data (R package SpadeR; Chiu et al. 2014; Chao and Jost 2015). Shannon diversity was estimated following Chao et al. (2013). Local contribution to beta diversity (LCBD; Legendre and De Cáceres 2013) was used to identify sites with unique fish assemblages (*beta.div* in package *adespatial*). Spearman's rank correlations were conducted for LCBD versus richness, estimated richness, and Shannon diversity.

Assemblage structure patterns

Assemblage structure based on species abundance and trait abundance was visualized using nonmetric multidimensional scaling (NMDS) in two dimensions using Bray-Curtis dissimilarities (*metaMDS* in package *vegan*). Species abundance and trait abundance were transformed to relative abundance per site to account for differences in fish abundance and stream width among sites (Clarke 1993). Species found at a single site or with less than 10 total individuals were excluded from multivariate analysis. Ordinations were evaluated according to stress, where values less than 0.2 indicated a two-dimensional representation is appropriate.

Univariate variation partitioning

Variation partitioning analysis using multiple regression (Borcard et al. 1992; Peres-Neto et al. 2006) determined the relative contribution of anthropogenic land cover at the three spatial scales (SW, SR, and R) to fish species richness, diversity, and LCBD. Land use variables measured at the three spatial scales were HUDEN, ROADDEN, %DEV, and %PastureHayCrops. A subset of local physical and chemical variables that were considered important indicators of fish habitat were also included in the analysis. These variables were reach width, reach elevation, stream slope, substrate size, canopy openness, discharge, temperature (mean, coefficient of variation, and maximum change in 15 min), ammonia, pH, specific conductivity, turbidity, and dissolved oxygen resulting in four groups of variables (SW, SR, R, and local fish habitat) in the analysis. Variable selection (R function *step)* was used to select variables for inclusion in each subset. Log Reach ROADDEN was selected

for estimated richness. No other land cover variables were selected at the watershed, riparian, or reach scale for any of the response variables; thus, a composite index of the sum of standardized land cover variables was used for each of the three spatial scales.

Redundancy analysis and variation partitioning

Variation partitioning analysis using redundancy analysis (RDA) was used to determine the relative contribution of anthropogenic land use at the three spatial scales (watershed (SW), riparian (SR), and reach (R)) and local fish habitat variables (see *Univariate variation partitioning* above) on the fish assemblage. Forward selection was used separately on each group of variables (alpha = 0.1, *forward.sel* in R package *adespatial*). No physical variables were selected for the trait analysis, so the physical variables selected for the species analysis were used. No

land cover variables were selected at the watershed, riparian, or reach scale, so a composite index of the sum of standardized land cover variables was used for each of the three spatial scales. The analysis was performed separately for fish taxonomic and trait assemblages. Species found at a single site or with less than 10 total individuals were excluded from the analysis. Species and trait abundances were Hellinger transformed prior to multivariate analyses. All statistical analyses were conducted using the R statistical language (R Core Team 2022) version 4.2.1.

Results

Environmental conditions

In general, streams were mildly acidic (mean pH = 6.7) with low turbidity (mean = 1.7 NTU, Table 2).

Table 2 Water chemistry of study streams. Abbreviations for stream names given in Table 1

Stream	Nitrate (mg/L)	Total phosphorus (mg/L P)	Ammonia (mg/L)	Ortho phosphate (mg/L)	E. coli (cfu/100 ml)	pH	Specific conductivity (µS/cm)	Turbidity (NTU)	Dissolved oxygen (mg/L)
Asneb	0.87	0.02	0.06	0.1	32.3	6.35	257.2	1.24	8.21
Broad	0.76	0.08	0.02			8.03	457	2.94	8.84
Catac	0.26	0.03	0.05	0.07	98.5	7	243.5	1.91	8.36
Fall	0.82	0.05	0.02	0.06	307.6	6.95	515	1.55	8.86
Falul	0.35	0.07	0.02	0.05	30.9	6.62	168.9	1.47	8.8
Flag	0.27	0.03	0.08	0.06	43.5	7.12	257.45	2.77	8.64
Gates	1.14	0.04	0.04	0.1	86.5	6.86	1002	0.91	8.91
Goodr	0.37	0.17	0.02	0.1		6.73	240.3	2.23	6.83
James	0.55	0.07	0.04	0.09	143.9	7.05	295.2	2.64	8.48
Monoo	0.91	0.03	0.04	0.06	127.6	6.65	435.5	1.56	8.86
Mulpu	0.64	0.02	0.04	0.09	27.9	6.56	256.3	1.28	9.71
Nod	0.26	0.04	0.02	0.08	131.4	6.67	274.4	0.01	9.34
Pearl	0.26	0.02	0.11	0.04	49.6	6.42	132.05	0.63	8.43
Phill	0.38	0.03	0.08	0.07	260.3	6.73	293.7	2.31	7.7
Reedy	0.69	0.03	0.07	0.12	172.3	6.56	250.3	1.46	8.25
Sucke	0.42	0.07	0.04	0.15	111.2	6.69	222.1	3.32	7.11
Trap	0.24	0.13	0.02	0.11	67.6	5.71	98.1	1.43	7.38
Trout	0.59	0.06	0.06	0.18	30.5	5.84	82.2	0.89	8.8
Waush	0.26	0.03	0.04	0.04	51.2	6.47	367.6	2.35	6.24
Wekep	0.46	0.02	0.03	0.06	62.4	7.09	465.05	2.74	8.82
Whitm	0.35	0.02	0.03	0.07	22.1	6.43	196.4	1.38	8.23
Willa	0.35	0.03	0.03	0.11	4	6.54	245.1	0.09	9.12
Average	0.51	0.05	0.04	0.09	93.1	6.69	307.1	1.69	8.36

Specific conductivity varied widely among streams and ranged from 82.2 to 1002 μS cm^{-1} with mean conductivity of 307.1 μS cm^{-1} (Table 2). Mean percent developed watershed area was 21% for the entire sub-basin but ranged from a low of 5% to a high of 63% among stream drainages (Table 1). Mean base-flow discharge was 1.02 m^3 s^{-1} (range = 0.01–9.10 m^3 s^{-1}) and average reach width was 4.6 m (range = 2.0–7.9 m). Mean summer 2020 stream temperatures ranged from 16.3 to 24.2 °C and there was substantial within- and between-stream variation (Fig. 2). Stream pH was positively associated with %Dev at the SR scale (Spearman's correlation coefficient rho = 0.69, adjusted p = 0.02), and specific conductivity was positively associated with %Dev at the SW scale (rho = 0.66, adjusted p = 0.03), ROADDEN at the SR scale (rho = 0.71, adjusted p = 0.02), and ROADDEN at the SW scale (rho = 0.78, adjusted p = 0.003).

Assemblage structure

Blacknose dace (*Rhinichthys atratulus*) were the most commonly collected fish (61.2% of individuals captured), and no other species made up more than 5% of the total abundance (N = 3778 fish, Table 3). Yellow bullhead (*Ameiurus natalis*), blacknose dace, bluegill (*Lepomis macrochirus*), white sucker (*Catostomus commersonii*), and common shiner (*Luxilus cornutus)* were the most widely distributed fish (59.1–77.3% of study sites). Observed species richness ranged from 2 to 12 species with an average of 6.4 species per site, while estimated species richness (observed species plus estimated unobserved species) ranged from 2 to 14.9 with an average of 7.7 species per site. Non-native fish species (bluegill, brown trout, largemouth bass (*Micropterus salmoides*), and yellow bullhead) comprised 7.4% of the total number of individuals, and the average number of non-native species per site was 1.7 (range 0–4).

The NMDS ordination of species abundance displayed a tight cluster of sites in the center left of the ordination space associated with high relative abundance of blacknose dace (Fig. 3A). A small cluster of sites in the lower right of the ordination space was associated with high relative abundance of common shiner, and a loose grouping of sites towards the right of the ordination space was associated with high relative abundance of yellow bullhead. The low stress value (0.08) indicated the two-dimensional space was a good representation of the distances among sites. In the NMDS

Fig. 2 Boxplots of daily mean temperature (°C) for study streams for June 21–July 16, 2020. The dark vertical lines are the median values, edges of the boxes represent 25% and 75% quartiles, and whiskers extend to data points up to 1.5 times the interquartile range. Data beyond 1.5 times the interquartile range are plotted individually. Stream name abbreviations defined in Table 1
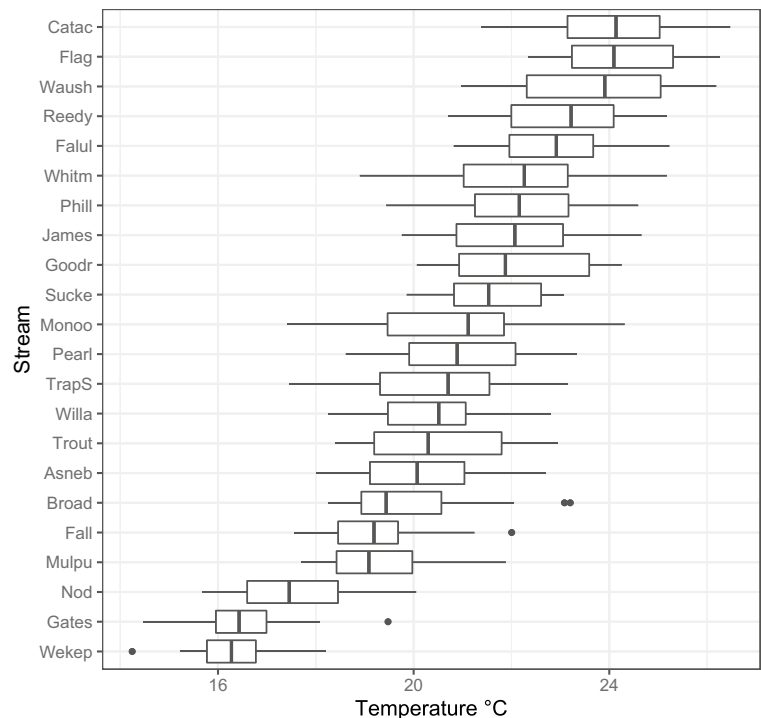
Table 3 Total percent abundance and percent occurrence for the 22 stream sites. Excluded brook, brown, and rainbow trout > 200 mm and all fish < 40 mm (see methods for explanation)

Species	Percent abundance	Percent of sites
Blacknose dace (*Rhinichthys atratulus*; Hermann, (1804), (BND))	61.2%	68.2%
Common shiner (*Luxilus cornutus*; Mitchill, (1817), (CS))	5.6%	59.1%
Atlantic salmon (*Salmo salar*; Linnaeus, (1758), (AS))	5.5%	4.5%
White sucker (*Catostomus commersonii*; Lacepède, (1803), (WS))	5.5%	68.2%
Longnose dace (*Rhinichthys cataractae*; Valenciennes, (1842), (LND))	5.4%	40.9%
Brook trout (*Salvelinus fontinalis*; Mitchill, (1814), (EBT))	4.8%	36.4%
Yellow bullhead (*Ameiurus natalis*; Lesueur, (1819), (YB))	4.2%	77.3%
Bluegill (*Lepomis macrochirus*; Rafinesque, (1819), (B))	2.7%	63.6%
Pumpkinseed (*Lepomis gibbosus*; Linnaeus, (1758), (P))	0.8%	31.8%
Fallfish (*Semotilus corporalis;* Mitchill, (1817), (F))	0.7%	13.6%
Golden shiner (*Notemigonus crysoleucas*; Mitchill, (1814), (GS))	0.7%	18.2%
Banded sunfish (*Enneacanthus obesus*; Girard, (1854), (BS))	0.6%	22.7%
Fathead minnow (*Pimephales promelas*; Rafinesque, (1820), (FHM))	0.5%	4.5%
Tessellated darter (*Etheostoma olmstedi*; Storer, (1842), (TD))	0.5%	22.7%
Chain pickerel (*Esox niger*; Lesueur, (1818), (CP))	0.5%	40.9%
Brown trout (*Salmo trutta*; Linnaeus, (1758), (BT))	0.3%	18.2%
Brown bullhead (*Ameiurus nebulosus*; Lesueur, (1819), (BB))	0.2%	22.7%
Largemouth bass (*Micropterus salmoides*; Lacepède, (1802), (LMB))	0.2%	13.6%
Creek chubsucker (*Erimyzon oblongus*; Mitchill, (1814), (CCS))	0.1%	4.5%
Yellow perch (*Perca flavescens*; Mitchill, (1814), (YP))	0.1%	9.1%
Total	$N = 3778$	$N = 22$

ordination of trait abundance, the sites were distributed across the ordination space, and the clear patterns from the species ordination were not evident (Fig. 3B). The two-dimensional solution was a good representation of the distances among the sites (stress = 0.04).

Univariate variation partitioning

Local physical conditions alone significantly explained the most variation (R^2adj = 30%, p = 0.015) in observed richness. Land cover at any scale did not explain a significant unique fraction of the variation (R^2adj < 0%, $p \geq$ 0.92). Variable selection retained log canopy openness. Observed richness was positively related to log canopy openness (slope = 1.43, se = 0.46, p = 0.005). Local physical conditions alone also explained the most variation in estimated richness (R^2adj = 22%, p = 0.024), whereas land cover at any scale did not explain a significant unique fraction of the variation (R^2adj $\leq$ 5%, $p \geq$ 0.17). Variable selection retained log canopy openness and log road density at the reach scale. Estimated richness was significantly related to log canopy openness (multiple regression slope = 1.76, se = 0.64, p = 0.013) but not log road density at the reach scale (multiple regression slope = −0.93, se = 0.58, p = 0.122).

For the Shannon index, local physical conditions alone did not explain a significant amount of variation (R^2adj = 15%, p = 0.109), and regardless of scale, land cover did not explain a significant unique fraction of the variation (R^2adj < 0%, $p \geq$ 0.475). Variable selection retained stream width and substrate. The Shannon index was significantly related to width (multiple regression slope = 0.15, se = 0.06, p = 0.024) but not substrate (multiple regression slope = −0.008, se = 0.004, p = 0.063).

Considering LCBD, local physical conditions alone did not explain a significant amount of variation (R^2adj = 21%, p = 0.097), and regardless of scale, land cover did not explain a significant unique fraction of the variation (R^2adj < 0%, $p \geq$ 0.77). Variable selection retained substrate, log discharge, and log canopy openness. LCBD was
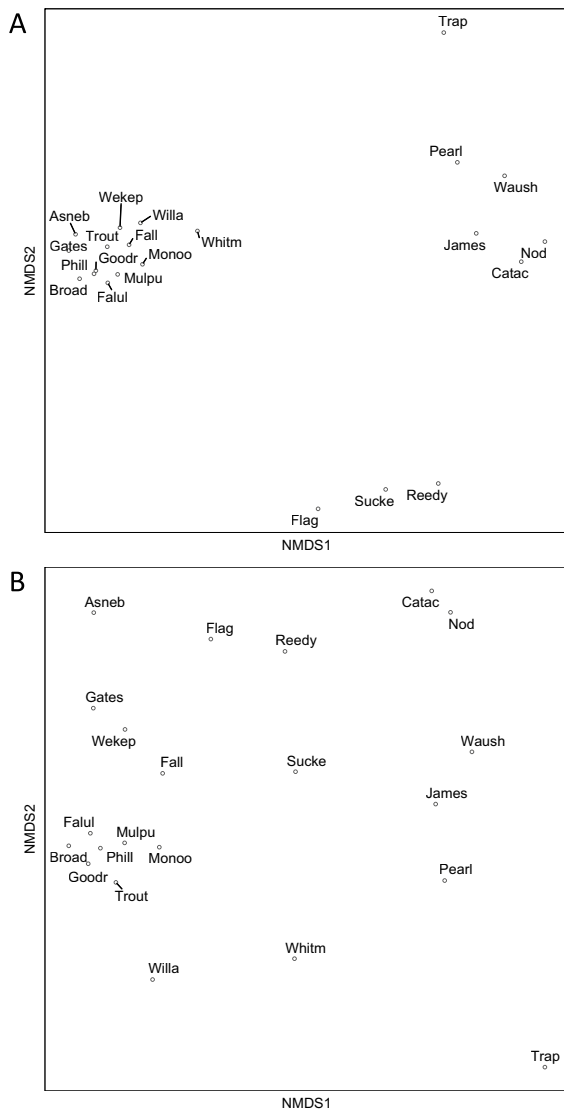
Fig. 3 NMDS ordination of species assemblage (stress = 0.08) (**A**) and trait assemblage (stress = 0.04) (**B**). Stream name abbreviations defined in Table 1, thin black lines connect text labels with sites

significantly associated with substrate (multiple regression slope = −0.0004, se = 0.0001, $p = 0.023$) but not log discharge (slope = 0.009, se = 0.007, $p = 0.20$) or log canopy openness (slope = −0.006, se = 0.003, $p = 0.10$). LCBD was negatively associated with observed richness ($rho = −0.48$, $p = 0.023$) and estimated richness ($rho = −0.48$, $p = 0.025$) but not with the Shannon index ($rho = −0.03$, $p = 0.90$).

Redundancy analysis and variation partitioning

The overall redundancy analysis for the taxonomic assemblage was statistically significant (R^2adj = 23.0%, $p = 0.015$), but only for the first axis (RDA 1 $p = 0.017$, all other $p \geq 0.97$). RDA 1 was associated with increasing ADMeanT and decreasing elevation and pH (Fig. 4A). RDA 1 was positively associated with yellow bullhead (goodness of fit (gof) = 0.41) and negatively associated with blacknose dace (gof = 0.56). Local physical conditions (elevation, ADMeanT, and pH) significantly explained the most variation in taxonomic structure (R^2adj = 28%, $p = 0.005$) and land cover at any scale did not explain a significant unique fraction of the variation (R^2adj < 0%, $p \geq 0.36$, Fig. 5A).

The overall redundancy analysis for the trait assemblage was statistically significant (R^2adj = 24.9%, $p = 0.047$), but only for the first axis (RDA 1 $p = 0.049$, all other $p \geq 0.98$). RDA 1 was associated with increasing ADMeanT and decreasing elevation and pH (Fig. 4B). RDA 1 was positively associated with macrophytes or vascular plant diet, maximum total length >30 cm but ≤ 64 cm, serial spawner, length of spawning season > 4 months, guarders; nest spawners, aquatic vegetation habitat, large woody debris habitat, lowland elevation, and slow current. RDA 1 was negatively associated with benthic feeder, non-serial spawner, length of spawning season > 2 but ≤ 4 months, nonguarders; brood hiders; lithophils, moderate current, and fast current. Local physical conditions (elevation, ADMeanT, pH) alone significantly explained the most variation (R^2adj = 28%, $p = 0.017$), and land cover at any scale did not explain a significant unique fraction of the variation (R^2adj ≤ 1%, SR $p = 0.064$, all other $p \geq 0.21$, Fig. 5B).

Discussion

The objective of this study was to compare the relative importance of urbanization at different spatial scales and local habitat conditions on both fish taxonomic and trait assemblages. We expected that these assemblages would be most sensitive to urbanization impacts in the watershed riparian zone and in the riparian zone of the sampled reach because of direct connections between land cover and stream habitat. Increasing urbanized land cover, especially at the

Fig. 4 Redundancy analysis biplots of taxonomic (**A**) and trait assemblages (**B**). Blue arrows and text indicate predictor variables, red vectors and text indicate fish species (**A**) or traits (**B**), and black open circles indicate stream sites. ADMeanT, average of mean daily stream temperature; Elev, site elevation; SW, subwatershed land cover; SR, stream riparian land cover; R, reach land cover. Trait abbreviations given in Table S1
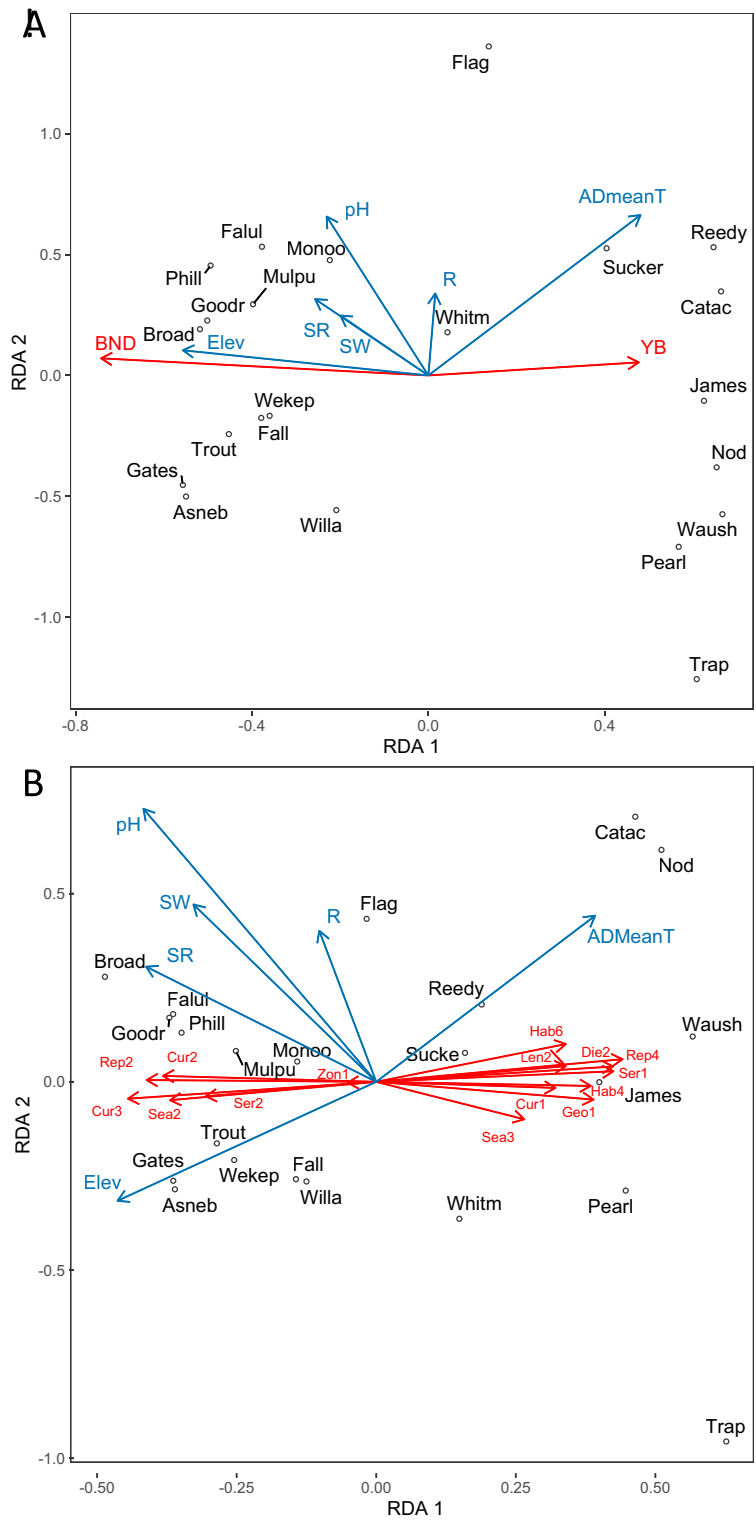
Fig. 5 Variation partitioning diagrams for physical (Phy), subwatershed (SW), stream riparian (SR), and reach (R) predictor variables on species (**A**) and trait (**B**) assemblages. Values represent adjusted R^2 values of unique (non-overlapping portions) or shared (overlapping portions) contributions to assemblage structure. Residuals represent unexplained variation, and adjusted R^2 values less than one are not shown
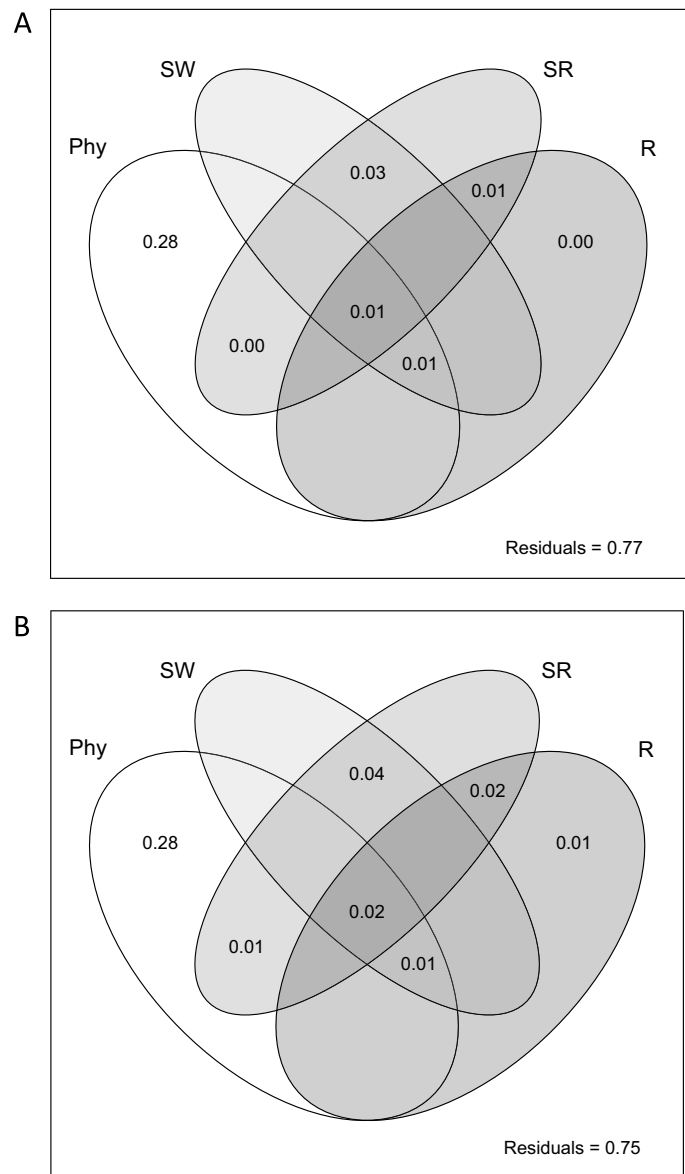
riparian and watershed scales, was associated with environmental changes relevant to fish in our study streams. However, anthropogenic land cover did not emerge as a major determinant of fish taxonomic or trait assemblage structure. Instead, site habitat conditions were most associated with taxonomic and trait assemblage structure.

Urbanized land cover was positively associated with specific conductivity and pH in our study streams at the two larger spatial scales, consistent with the urban stream syndrome (Walsh et al. 2005; Utz et al. 2016). Increased conductivity is likely

due to winter road salt application and runoff from impervious cover (Koryak et al. 2001; Kaushal et al. 2021). Summer base flow conductivity in six of our study streams exceeded the 300 uS/cm benchmark for macroinvertebrate impacts identified in Clements and Kotalik (2016) and Cormier et al. (2018), with one site exceeding 1000 us/cm.

Local physical conditions alone were associated with species richness, diversity, and LCBD. Univariate partitioning analyses for both observed and estimated richness found that local physical conditions alone explained the most variation, and

canopy openness was positively related to species richness. Similarly, species diversity was positively associated with stream width, but not land cover, at larger spatial scales. These patterns make sense, as larger areas (as measured by width) and more openness likely provide more niches, microhabitats, and overall food abundance, thereby supporting an overall larger number of species. However, the overall finding that only the local scale seemed important surprised us. Studies in different regions and at varying spatial scales have found conflicting results concerning the relative importance of local conditions and anthropogenic impact on fish assemblages. For example, Wang et al. (2001) found that connected watershed impervious surface area explained 55% of species richness and 50% of species diversity in streams in southeast WI, USA. Effects on stream fishes were greatest for land cover within the riparian buffer versus further away, and 12% connected imperviousness appeared to be a threshold for diverse fish assemblages (Wang et al. 2001). In the Upper Paraná river basin in Brazil, Borges et al. (2020) found that fish dispersal, environmental variables, and anthropogenic land cover were all important in explaining stream fish richness and LCBD values. In our study, LCBD was negatively associated with substrate size but not land cover at larger spatial scales. Large LCBD values represent assemblages that are most different from typical assemblages, and thus can indicate unique diverse assemblages or disturbed low richness ones (Legendre and De Cáceres 2013; Legendre 2014). As in Lopez-Delgado et al. (2020) and Heino and Grönroos (2017), LCBD was negatively associated with species richness, indicating that high LCBD values tended to indicate sites with unique and low richness assemblages.

Taxonomic assemblage structure was associated with stream temperature, pH, and elevation. The taxonomic assemblage RDA identified a gradient with higher elevation, less acidic, and cooler sites dominated by blacknose dace, while lower elevation, more acidic, and warmer sites were dominated by yellow bullhead. Higher elevations typically have higher water velocities than lower gradient low elevation sites. Thus, the taxonomic assemblage appears structured along an axis of preference for increasing current, with those favoring fast current (like blacknose dace) on one end and species that inhabit

sluggish areas (such as yellow bullhead, banded sunfish (*Enneacanthus obesus*), and bluegill) on the other end. Current is critically important to fish species, as it impacts many aspects impacting their biological fitness, such as ability to forage (Piccolo et al. 2008; Sliger and Grossman 2021), anti-predator behavior (Fu et al. 2014), and reproduction (Banet et al. 2016; Bartoň et al. 2021). Similarly, temperature is a well-recognized factor structuring stream fish assemblages (Brazner et al. 2005; Beauchene et al. 2014). June–July temperatures in our streams spanned the cold water (< 18.29 °C), cool water (18.29–21.70 °C), and warm water (> 21.70 °C) categories identified by Beauchene et al. (2014) for Connecticut stream fish assemblages using June–August temperatures. Changes in stream thermal regime have been associated with impervious surface area (e.g., Hassett et al. 2018), stormwater pipes, and lack of riparian tree cover (Nelson and Palmer 2007; Timm et al. 2021). Increased developed land cover leads to elevated stream temperatures and greater temperature fluctuations (Hassett et al. 2018), though our study design was unable to separate anthropogenic impacts from underlying natural environmental variability.

Stream temperature, pH, and elevation were also associated with trait assemblage structure. In the trait assemblage RDA, an increase in mean temperature and a decrease in elevation were positively associated with traits related to habitat (lowland elevation, slow current, aquatic vegetation, large woody debris) and diet (macrophytes or vascular plant diet) along with traits related to reproductive biology (serial spawner, long spawning season, guarders; nest spawners) and medium maximum length. Increasing elevation and decreasing temperature were positively associated with traits related to habitat (moderate and fast current, benthic feeder) and reproduction (non-serial spawners, nonguarders; brood hiders; lithophils, medium spawning season length). Some of these associations are unsurprising, such as traits related to faster currents in higher elevations. Other studies have found that variation in fish traits is associated with both local (e.g., in-stream habitat) and landscape (e.g., longitudinal gradients) factors (e.g., Goldstein and Meador 2004; Pease et al. 2012). One limitation of our study is that we did not account for phylogenetic relatedness. For example, Cano-Barbacil et al. (2022) found lithophilic species at higher elevations, but found that it was related to shared evolutionary

history of these species and elevation was not significant after controlling for phylogenetic relatedness.

Contrary to our expectations, urbanized land cover at any scale was not a major determinant of taxonomic or trait assemblage structure in this study. In a study of 29 streams in Hungary, Czeglédi et al. (2020) found that the downstream species pool and local stream characteristics, rather than urbanization, were most important in explaining fish assemblage structure. In contrast, Brown et al. (2009) found that increasing watershed urbanization (based on housing density, percent developed land, and road density) was associated with altered stream fish assemblages in the Boston metropolitan area. Armstrong et al. (2011) found impervious cover was negatively associated with brook trout relative abundance, and Kanno et al. (2015) found watershed forest cover was positively associated with brook trout occurrence. Our study within a single sub-basin across a gradient of increasing urbanization found that higher elevation streams with high levels of watershed and riparian urbanized land cover could still support pollution-intolerant fish (e.g., brook trout, brown trout) populations.

Conclusions

Our results illustrate the importance of examining multiple spatial scales simultaneously. Urban land cover was associated with aspects of physical stream health at the two largest spatial scales (riparian and watershed scales), while fish taxonomic and trait assemblages were only associated with variables measured on the smallest spatial scale. This does not mean that anthropogenic impacts on fish assemblages were unimportant, since urban land cover may indirectly affect fish assemblages by modifying local habitat conditions (i.e., Booth 2005). While the current study examined the fish assemblage, it is also important to consider other measures of ecological health (macroinvertebrates, algae, etc.) that might respond differently to urban impacts (e.g., Lammert and Allan 1999). Incorporating impacts of urbanization on both fish taxonomic and trait assemblage structure is essential to stream conservation.

Authors' contribution Study design and methodology: John P. Ludlam, Daniel P. Welsh, Elizabeth S. Gordon, Benjamin Levy, Jane Huang, Aisling M. O'Connor; statistical analysis: John P. Ludlam; writing—original draft preparation: John P. Ludlam, Daniel P. Welsh; writing—review and editing: John P. Ludlam, Daniel P. Welsh, Elyse V. Clark, Emma L. Downs, Elizabeth S. Gordon, Benjamin Levy; funding acquisition: Elizabeth S. Gordon, Jane Huang, Aisling M. O'Connor.

Declarations

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