Relative effects of local- and landscape-scale environmental factors on stream fish assemblages: evidence from Idaho and Ohio, USA

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With 4 figures and 1 table

Abstract: Despite increased attention to spatial considerations in catchments, the importance of both environmental factors and spatial context in understanding stream fish assemblages is not fully resolved. This study explored the relative influences and spatial relationships of environmental factors at landscape (i.e., catchment) and local (i.e., reach) scales on characteristics of stream fish assemblages including species richness ($S$), diversity ($H'$), evenness, and $1/D$), density and biomass, and composition (% top carnivores and % benthic insectivores). We conducted this research in two geographic regions (northern Idaho and Ohio, USA) characterized by distinct environmental attributes. Using a partial constrained ordination approach, we found that pure spatial factors explained 26% of fish assemblage variation in Ohio (OH) and 18% in Idaho (ID). Shared (spatially-structured) environmental variables explained more variation in fish assemblages in ID (28.6%) than in OH (20.7%). The influence of pure (non-spatial) environmental characteristics accounted for nearly 24% of the variation observed in fish assemblages in OH catchments, whereas pure environmental factors accounted for 31% of assemblage variation in ID. Within the pure environmental component, the influence of local, landscape, and joint (i.e., combined effects of environmental variables from both spatial scales) effects accounted for relatively equal amounts of assemblage variation for both study regions. However, local-scale variables were slightly more important in ID, whereas joint influences were more important in OH. Taken as a whole, our results suggest that a complex suite of spatial and environmental factors influenced fish assemblages but that the relative importance of these components differed in each of our study areas. The strong influence of spatial patterns in our results reveals the importance of integrating spatial context into studies predicting fish assemblage characteristics. The contrasting findings between geographic regions encourage additional research efforts that address regional variability in multi-scale environmental influences on fish assemblages.

Key words: species richness, diversity, density, biomass, composition, shared environmental variables, pure environmental factors, spatial patterns.

Introduction

Understanding, characterizing, and predicting local biological assemblages represent significant challenges to ecologists. In stream ecosystems fish assemblages are structured by multiple factors that often operate at different spatial and temporal scales (Lammert & Al- lan 1999, Sutherland et al. 2002, Walters et al. 2009). These factors act independently and in concert to constrain the presence and distribution of stream fishes through a hierarchy of nested environmental filters (Poff 1997). Coarse variation in species composition among assemblages is derived from geographically-unique species pools (Angermeier & Winston 1998).
that are thought to differ based largely on historical patterns of dispersal and speciation (Ricklefs 1987). For instance, due to duration of time available for speciation, environmental conditions, and refuge opportunities created by directional orientation of major drainages, streams east of the Rocky Mountains (USA) typically exhibit greater diversity in their respective species pools than those west of the Rocky Mountains (Moyle & Herbold 1987, Moyle & Cech 2002).

The spatial hierarchy of physical and biological stream attributes has been well described at the catchment scale (Frissel et al. 1986, Montgomery 1999). For example, Vannote et al.’s (1980) River Continuum Concept related longitudinal shifts in carbon and energy sources (i.e., allochthony vs. autochthony) to changes in fish assemblage structure. Other investigators have shown that increased species richness and shifts in trophic structure are concurrent with increases in stream size, catchment area, and habitat volume (Newall & Magnuson 1999). Further evidence also suggests that fish assemblages vary by position within the stream network (Smith & Kraft 2005), especially relative to distance from major tributary mouths or from larger, mainstem rivers, which can introduce species typical of larger streams to small stream assemblages (Gorman 1986, Osborne & Wiley 1992).

In spite of this current understanding, the relative influence of environmental characteristics at different spatial scales remains largely unresolved (see Allan et al. 1997, Townsend et al. 2003). In particular, investigations of landscape- versus local-scale environmental characteristics on aquatic assemblages have yielded mixed results. Some investigators suggest that broad, landscape-scale properties, such as catchment land use and land cover (LULC) better predict in-stream conditions (Roth et al. 1996, Johnson et al. 1997) and fish assemblage characteristics (Jones & Grant 1996, Richards et al. 1996, Allan et al. 1997). For example, working in distinct biogeographic regions, Pease et al. (2011) and Esselman & Allan (2010) found strong effects of both landscape-scale (e.g., catchment land cover) and local-scale (e.g., in-stream habitat) factors on stream fish assemblage structure. Others have found finer-scale, reach-level factors including riparian LULC characteristics (Sponseller et al. 2001), in-stream habitat (Meffe & Sheldon 1988, Talmage et al. 2002, Rowe et al. 2009), and water quality (Meador & Goldstein 2003) to be more influential on stream biota. Furthermore, the hierarchical nature of stream ecosystems suggests that biological communities are spatially-structured as well and characteristics of local assemblages are influenced not only by spatial position but also underlying spatial structure of environmental conditions (Dray et al. 2006).

In this study, we explored relationships between fish assemblages and environmental characteristics at the local (i.e., reach) and landscape (i.e., catchment) scales, as well as the effect of spatial influences (i.e., relative spatial distribution of study sites and underlying spatial structure of environmental factors) on stream fish assemblages. We chose two distinct regions of the continental USA (Idaho – ID and Ohio – OH), each representing unique climatic and physiographic regions, for our study. We synthesize results from this descriptive effort to propose future research directions that may be fruitful in further understanding the variability of multi-scale environment-fish relationships in differing biogeographic contexts.

Methods

Study areas

We surveyed sixteen stream reaches in northern ID (2006–2007) and sixteen in southern OH (2009) (Fig. 1). Study catchments were selected to represent dominant landscapes (defined by geology and LULC) of each region and individual study reaches were selected to be largely representative of overall catchment LULC. Our northern ID study region is mountainous with a maritime-influenced climate, dominated by extensive coniferous forests and highly erodible volcanic ash deposits (McGrath et al. 2002). In OH, rolling glaciated plains consisting of rich, loamy soils and extensive glacial deposits characterize the western part of our OH study area (Griffith et al. 2008). Forests and prairie historically covered this section of the state, however, today, large-scale agriculture and urban development dominate the landscape (Griffith et al. 2008). In general, landscapes in the eastern part of our OH study area are unglaciated, hilly, and largely covered with second-growth mixed oak forests.

Fish surveys

Based on a geomorphic process approach, we established reach lengths to be 20 X mean bankfull width (Kondolf & Micheli 1995). We surveyed fish assemblages using a Smith-Root® LR24 backpack electrofisher, blocking each reach with fine-mesh nets to prevent fish emigration or immigration while electrofishing. Given our assemblage-level assessment, we aimed for a 70% depletion, which usually required 3–4 passes. Because we would have been unlikely to achieve a depletion of 70% for all species in the entire assemblage, we chose common species to measure our depletion level in the field [ID, salmonid species; OH, creek chub (Semotilus atromaculatus) or bluntnose minnow (Pimephales notatus), depending on dominance]. Following capture, we weighed (g) and identified each individual fish to species. All fish were held in aerated live-wells until they were released back into the stream following processing. We completed all fish surveys during low flow periods of the summer and early fall.
Local variables

Our local-scale environmental variables were bounded by the extent of the reach. We characterized in-stream, bank, and riparian habitat using a combination of quantitative and semi-quantitative methods. Because of the relative importance of wood in fluvial systems, we counted all pieces of large woody debris (LWD; \( > 0.1 \text{ m} \times 1.0 \text{ m} \)) within the bankfull channel (Montgomery et al. 1995). We used a hybrid assessment of stream condition derived from the Idaho Small Stream Ecological Assessment Framework (Grafe 2002) and the Vermont Rapid Habitat Assessment (VTDEC 2003) to evaluate habitat quality in our ID streams. The resulting Idaho Rapid Habitat Assessment (IRHA) incorporated the abiotic ID evaluation descriptors within the Vermont assessment framework to provide a more quantitative protocol designed to target habitat homogenization across the reach (Plafkin et al. 1989, Barbour et al. 1999, Sullivan & Vierling, in press). We used the Ohio Qualitative Habitat Evaluation Index (QHEI) for OH study reaches (Rankin 2006). Both assessment protocols were designed to evaluate habitat heterogeneity within the study reach and subsequently, both focus on similar metrics relative to the quality of in-stream, nearshore, and riparian habitat. Higher scores (IRHA 0–200; QHEI 0–100) indicate better quality habitat overall.

We conducted cross-sectional surveys at equidistant lateral transects where we measured bankfull width, wetted width, mean water depth, and mean bankfull depth (e.g., the depth at which a stream has reached the top of its banks). We quantified median sediment size \( (D_{50}) \) using pebble counts following the Wolman method (1954). We used a Rapid Geomorphic Assessment (RGA) protocol to evaluate geomorphic condition based on channel adjustment processes (VTDEC 2003). Due to the differing geological contexts and valley settings, we used the base RGA protocols developed for unconfined streams in OH and for confined streams in ID. Both protocols assess four geomorphic adjustment categories: degradation, aggradation, widening, and change in planform. Based on field indicators of sediment accumulation, presence of bars, bank erosion, bed scour, and other indicators of adjustment, we scored each category from 0 to 20, where 0 represented significant channel adjustment and gross deviation from expected geomorphic conditions; total RGA scores ranged from 0 to 80.

Although our focus was on physical abiotic variables, we remained aware of the potential influences of water quality on fish assemblages (Meador & Goldstein 2003, Esselman & Allan 2010). Water quality concerns in our ID catchments primarily relate to sedimentation (Rowe et al. 2003), although legacy heavy-metal effects have been reported in some locales (Maret
& MacCoy 2002). Potential influences of water quality on fish species were likely of greater concern in OH given the prevalence of urban and agricultural land uses. We attempted to limit the potential effects of water-quality through thoughtful experimental design including careful selection of reaches that had intact vegetated riparian buffers and no contaminant point sources within or upstream of the reach. We measured pH and conductivity at three points (left bank, mid-channel, right bank) at the bottom, middle, and top of each reach using a YSI 650 MDS® with a 600 R® sonde. From these sub-sampling locations, we generated mean pH and conductivity estimates for each reach.

**Landscape variables**

The landscape was bounded by the spatial extent of the catchment upstream from the outlet point of each of our study reaches. We calculated drainage area of the catchment and landscape-scale characteristics using ArcGIS® 9.3 (ESRI, Redlands, CA, USA). We selected variables that characterized predominant LULC and used land-cover data from the National Land Cover Dataset (USGS 2001) to quantify % development (i.e., % developed open space + % low-density development + % medium-density development), % high-density development, % barren land, % impervious surfaces, % forest (i.e., deciduous, evergreen, and mixed forest combined), % shrub/scrub, % grassland, % pasture/hay, % crops, and % wetlands in each study catchment. We measured the degree of canopy closure of forested sections by quantifying the area comprised of moderate (26–50 %) and high (76–100 %) canopy coverage. Little, if any, developed land cover was present in our ID study catchments largely due to the rugged topography, climate, and remoteness of the area. However, timber harvest operations and recreational use are prevalent in the region and this has led to an extensive network of roads across the landscape. We used road density (km · km–2) in the catchment as a measure of development in our ID study region.

**Spatial variables**

We used a Principal Coordinates of Neighbors Matrix (PCNM) approach to generate a set of spatial variables (Borcard & Legendre 2002). The PCNM is generated from a Euclidean distance matrix based on the latitudinal and longitudinal coordinates of each study reach. The PCNM axes provide a method to describe underlying spatial structure of the sample sites across the entire range of scales present in the study design. The PCNM results can be used to uncover significant spatial relationships among sample sites and biological data. This method is often considered an improvement on trend surface analysis, which only accounts for coarse spatial variation at the broadest scales represented in the data set, and can therefore be less effective in modeling fine-scale relationships (Borcard & Legendre 2002, Dray et al. 2006).

**Numerical analysis**

We calculated fish density (number · m–2) and generated biomass estimates (g · m–2) based on surface area (mean wetted width × reach length) of each study reach. We measured fish assemblage diversity using species richness (S), Shannon-Weiner’s Informational Index ($H'$) (Shannon & Weaver 1949), evenness (E), and Simpson’s Diversity Index (1/D) (Simpson 1949). $H'$ increases, based in part, on total number of species counted, but the relative density of each species is also taken into account, thereby incorporating a measure of heterogeneity. Simpson’s index is a measure of dominance and quantifies the degree to which individuals are concentrated in a few species. Given the differences in sampling area among our reaches and the inherent relationship between species richness and habitat area (Angermeier & Schlosser 1989), we applied a species-area equation following Preston (1960) to adjust our final diversity measures. Using Barbour et al. (1999) as a guide, we selected the following guilds to further characterize fish assemblage composition: % top carnivores [largemouth bass (Micropterus salmoides), smallmouth bass (Micropterus dolomieui), and rock bass (Ambloplites rupestris) – OH] or % ‘catchable’ salmonid species (ID); and % benthic insectivores [e.g., sculpin species (ID and OH), darter species (OH), sucker species (OH), madtom species (OH), and benthic-oriented cyprinid species (OH)].

**Statistical analysis**

We arranged our three sets [landscape, local, and spatial (derived from PCNM)] of explanatory variables into separate matrices for use in a partial constrained ordination analysis. Partial constrained ordination was a relevant statistical approach in this case as it allowed us to quantify the relative contributions of both pure and shared influences of groups of explanatory environmental variables (Anderson & Gribble 1998). Prior to variance partitioning procedures, we performed steps to minimize the overall degree of colinearity among variables and attain the appropriate number of predictor variables (i.e., sample size – 1; ter Braak & Verdonschot 1995) for use in a constrained ordination. We created pairwise correlation matrices separately for local and landscape variables for each study region and identified pairs exhibiting Pearson correlation coefficients (r) > 0.80. In the event of significant correlations, we retained only one of the two variables. The retained variable was chosen based on our judgment of its relative predictive potential.

In partial constrained ordination, either canonical correspondence analysis (CCA) or redundancy analysis (RDA) are used based on the inherent relationship between the observed biological parameters and environmental gradients; linear relationships dictate the use of RDA, unimodal responses require CCA. We ran detrended correspondence analysis (DCA) with our environmental and fish data to determine which constrained ordination analyses to use (ter Braak & Verdonschot 1995). Results of gradient lengths along the first DCA axis from both our OH and ID fish assemblage datasets were < 2 standard deviations, indicating that RDA was the appropriate ordination technique (ter Braak & Verdonschot 1995).

We used forward selection to identify significant predictors (Blanchet et al. 2008). We ran 1000 permutations of Monte Carlo tests to identify significant predictors. We retained only significant predictor variables, thereby reducing the total number of variables across the three explanatory matrices (local, landscape, and spatial) to < 15 for each study region. We retained three (habitat score, LWD, and conductivity) of seven local-scale environmental variables in our ID dataset and five (bankfull depth, RGA, LWD, $D_{50}$, and pH) of seven local-scale variables in our ID dataset. We retained, four (drainage area, % development, % wetlands, and % pasture/hay) of fourteen landscape-scale variables from our OH dataset and four (drainage area, road density, % forest, and % shrub/scrub) of eleven landscape-scale variables from our ID dataset. Relatively few of the original landscape-scale variables were retained for
use in our final analyses due in part to the strong associations among LULC types in our study catchments.

Variance partitioning required twelve runs ([run] constraining variable(covariables)): [1] local; [2] landscape; [3] spatial; [4] local(landscape); [5] local(spatial); [6] local(landscape + spatial); [7] landscape(local); [8] landscape(spatial); [9] landscape(local + spatial); [10] spatial(local); [11] spatial(landscape); and [12] spatial(local + landscape). This method partitions the total variation of the fish assemblage dataset into components that are explained by local, landscape, and spatial predictors, as well as the relative amount of variation explained by each explanatory matrix when one or both of the other matrices are partialled out as covariables (Anderson & Gribble 1998). Using this approach, we first partitioned total variation in fish assemblage composition into four components: pure environmental, pure spatial, shared (i.e., spatially-structured environmental), and unexplained. To quantify the influence of environmental factors at landscape and local scales, we subsequently partitioned out the three components of pure environmental variation (i.e., local, landscape, and joint). We visually displayed select ordination results by creating biplots for OH and ID environment-fish datasets. We created separate biplots illustrating the correlations between fish assemblage metrics and pure environmental variables from local- and landscape-scale datasets.

We used JMP 9.0 (SAS Institute Inc., Cary, IN) statistical software for all summary statistics and correlation analyses, Canoco 4.5 (Microcomputer Power, Ithaca, NY) for our ordination analyses, and CanoDraw 4.5 (Microcomputer Power, Ithaca, NY) for the biplots.

Results

Fish assemblages

Fish assemblages were markedly different between our two study regions (Table 1), as was expected considering the unique climatic, geological, and biogeographic settings. We surveyed a total of 42 species from OH study reaches, whereas we observed only 16 species in ID. Overall, assemblages were characterized by higher diversity in OH than in ID. Although mean fish density

| Table 1. Summary statistics for multi-scale environmental variables and fish assemblage characteristics from the 32 study catchments in OH and ID, USA. |
|-------------------------------------------------|-----------------------------------------------|
| Fish assemblages                               |                                              |
| \( S(\text{adjusted for area}) \)              | [OH] 11.17 - 15.26 [ID] 1.24 [SD] 1.23       |
| \( H^\prime \)                                 | [OH] 1.14 - 2.52 [ID] 0.55 [SD] 0.36         |
| \( E \)                                       | [OH] 0.63 - 0.77 [ID] 0.27 [SD] 0.37         |
| \( 1/D \)                                      | [OH] 1.13 - 1.54 [ID] 0.87 [SD] 0.91         |
| Density (number m\(^{-2}\))                    | [OH] 0.03 - 0.64 [ID] 0.24 [SD] 0.02         |
| Biomass (g m\(^{-2}\))                        | [OH] 0.37 - 12.59 [ID] 3.19 [SD] 3.07        |
| % Top carnivores                              | [OH] 40.00 - 22.00 [ID] 3.40 [SD] 6.20       |
| % Benthic insectivores                        | [OH] 12.00 - 71.00 [ID] 47.10 [SD] 20.50     |
| Local-scale variables                         |                                              |
| Bankfull depth (m)                            | [OH] 0.25 - 0.59 [ID] 0.40 [SD] 0.09         |
| \( D_0 \) (mm)                                | [OH] 0.50 - 67.00 [ID] 25.00 [SD] 14.70      |
| LWD (number m\(^{-2}\))                       | [OH] 0.02 - 0.18 [ID] 0.08 [SD] 0.04         |
| RGA (out of 80)                               | [OH] 42.00 - 66.00 [ID] 55.50 [SD] 6.40      |
| Habitat score (%)                             | [OH] 51.00 - 84.00 [ID] 68.80 [SD] 9.30      |
| Stream order                                 | [OH] 2.00 - 4.00 [ID] 2.90 [SD] 1.90         |
| Conductivity (\(\mu S\) cm\(^{-2}\))         | [OH] 224.00 - 1368.00 [ID] 689.00 [SD] 284.00 |
| pH                                           | [OH] 7.90 - 8.40 [ID] 8.20 [SD] 0.20         |
| Landscape-scale variables                    |                                              |
| Drainage area (km\(^2\))                     | [OH] 4.30 - 372.50 [ID] 70.10 [SD] 88.70    |
| % Development                                | [OH] 3.30 - 78.10 [ID] 160.00 [SD] 20.80     |
| Road density (km km\(^2\))                   | [OH] - - - [ID] - - - [SD] - - -           |
| % High-density development                   | [OH] 0.00 - 20.60 [ID] 1.50 [SD] 5.10       |
| % Forest                                     | [OH] 0.40 - 83.70 [ID] 27.40 [SD] 28.40     |
| % Grassland                                  | [OH] 0.00 - 1.60 [ID] 0.80 [SD] 0.50         |
| % Pasture/Hay                                | [OH] 0.00 - 33.20 [ID] 12.40 [SD] 10.90     |
| % Crops                                      | [OH] 0.00 - 92.80 [ID] 41.40 [SD] 34.90     |
| % Wetlands                                   | [OH] 0.00 - 0.40 [ID] 0.10 [SD] 0.10         |
| % Impervious                                 | [OH] 0.30 - 70.40 [ID] 10.40 [SD] 18.70     |
| % Moderate canopy                            | [OH] 0.30 - 6.60 [ID] 3.10 [SD] 2.00        |
| % High canopy                                | [OH] 0.30 - 76.10 [ID] 22.80 [SD] 25.10     |

The landscape-scale environmental factor effects on stream fish assemblages are marked due in part to the strong associations among LULC types in our study catchments.
was similar, the comparatively large SD of fish density in our ID study area was largely an artifact of the high abundances of various sculpin species found at a few reaches. Biomass was greater in OH assemblages than in ID assemblages although results may have been inflated by the high biomass measured at one reach that contained a number of large, heavy-bodied common carp (*Cyprinus carpio*). ID assemblages were dominated by a suite of salmonid species [e.g., bull trout (*Salvelinus confluentus*), brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*), westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), and cutthroat × rainbow hybrid trout (*O. clarkii lewisi* × *O. mykiss*)] and in some cases, northern pikeminnow (*Ptychocheilus oregonensis*) as top carnivores. In contrast, we found OH fish assemblages to be comprised of relatively few top carnivores. Benthic insectivores, including central stoneroller minnow (*Campostoma anomalum*) and various darter species, sucker species, and bullhead species dominated OH assemblages.

**Environmental-fish relationships**

We found substantial variability in the environmental conditions at the local- and landscape-scales in each study region (Table 1). Our partial constrained ordination results illustrated that the relative effects of environmental factors and spatial influences on fish assemblages were different between the two study regions as well. Overall, a larger proportion of assemblage variation was accounted for in our ID dataset (76.7%) than in our OH dataset (69.8%). The proportion of assemblage variation accounted for by pure spatial influences (i.e., spatial patterns not shared by environmental data) was larger in OH (25.5%, *p* = 0.018) than in ID (17.5%, *p* = 0.002) (Fig. 2). However, the influence of spatially-structured environmental vari-

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**Fig. 2.** The proportion of variation in fish assemblage characteristics accounted for by pure spatial factors (derived from a principal coordinates of neighbor matrices approach), shared (spatially-structured) environmental variables, and pure (non-spatial) environmental variables. Proportions of explained variation were obtained from variance partitioning procedures in partial RDA. Also illustrated (in call-outs) are the relative amounts of the pure, non-spatial environmental variation accounted for by local, landscape, and joint (i.e., variation shared by both local and landscape-scale variables) influences. The left column shows results for Ohio and the right column for Idaho.
Landscape-scale environmental factor effects on stream fish assemblages

Variables (i.e., variation shared by both spatial and environmental factors) was more important in ID (28.6%) than OH (20.7%). Pure environmental factors (i.e., local and landscape variables with spatial influences partialled-out) accounted for more variation in ID (30.6%, \( p = 0.002 \)) than OH assemblages (23.6%, \( p = 0.168 \)).

When we explored the influence of pure environmental factors in greater detail (i.e., pure local-scale, pure landscape-scale, and joint influences of local- and landscape-scale factors) we found that local-scale factors accounted for a larger proportion of variation in ID than in OH fish assemblages (Fig. 2). In contrast, the effect of pure landscape-scale factors was similar between study regions. Joint influences (i.e., variation that can be explained by either local or landscape factors) accounted for a larger relative proportion of assemblage variation in OH, suggesting that fish assemblages and local conditions are responding to similar underlying gradients present at broader, landscape scales.

We illustrated several key environment-fish relationships in our ordination biplots. At the landscape scale in OH, fish assemblage richness was strongly correlated with drainage area (+) (Fig. 3a). Fish assemblage \( H' \), % carnivores, and assemblage biomass were all negatively associated with pasture/hay, and to some degree, catchment development. The ID assemblage-landscape biplot illustrated a positive relationship between drainage area and species richness, similar to OH (Fig. 3b). The landscape biplot for ID also illustrated key positive relationships between (1) shrub/scrub land cover and assemblage biomass, % carnivores, \( 1/D \), and (2) forest cover and assemblage density and % benthic insectivores. Our OH assemblage-local biplot highlighted positive relationships between assemblage dominance (\( S \), \( H' \), and \( E \)) displayed a negative relationship with habitat scores. In ID, at the local scale, multiple fish assemblage metrics most closely aligned with measures of geomorphic condition and median sediment size (Fig. 4 b). However, the proportion of carnivores in the assemblage was more closely associated with both pH and bankfull depth (+).

Fig. 3. RDA biplots highlighting relationships between landscape-scale environmental variables and fish assemblage characteristics for (a) OH and (b) ID. Solid arrows indicate the direction of increase for fish assemblage variables and dashed arrows indicate how environmental variables were ordinated.
Discussion

Understanding the concurrent influences of environmental factors at both landscape and local scales is becoming increasingly important in the monitoring, assessment, and conservation of stream fish assemblages. In this study, we explored the relative influence of spatially-explicit environmental factors on fish assemblages in catchments of ID and OH. Our results strongly point to the importance of integrating the spatial context of the study sites in predicting fish assemblage characteristics. Our findings also indicate that the relative influence of both spatial and environmental variables on fish assemblage variation can be markedly different in unique biogeographic regions. Taken as a whole, our findings contribute to a growing body of literature addressing multi-scale fish-environment relationships in differing biogeographic contexts.

Spatial relationships

A more complete understanding of complex multi-scale influences of environmental characteristics on fish assemblages requires that, in addition to linking spatially-explicit environmental attributes with fish assemblages, we simultaneously consider the influence of spatial patterns in fish assemblages relative to both the distribution of environmental variables and the distribution of the assemblages themselves. This is important for two primary reasons. Firstly, although spatial correlations and ecological patterns and processes are largely thought to be scale-dependent, few aquatic studies have simultaneously evaluated the associations between different levels of spatial scale and biotic community patterns and the influence of spatial structure on these relationships (but see Magalhães et al. 2002, Esselman & Allan 2010, Sály et al. 2011). Second, potential covariation between anthropogenic activities and natural landscape attributes can lead to an overestimation of land-use effects (Allan 2004), suggesting that correlations between human development and natural landscape gradients might also be expected to vary with the scale of observation. For example, Wang et al. (2001) showed that the influence of impervious surfaces varied relative to the distance from the sampling location.

In our study, spatial factors represented the predominant influence on fish assemblages with pure spatial and shared (spatially-structured) environmental variables cumulatively explaining ~46% of the variation in fish assemblage characteristics in both study areas.

Fig. 4. RDA biplots highlighting relationships between local-scale environmental variables and fish assemblage characteristics for (a) OH and (b) ID. Solid arrows indicate the direction of increase for fish assemblage variables and dashed arrows indicate how environmental variables were ordinated.
However, the relative influences of pure and shared spatial variation were different for each region. In OH, the greater influence of pure spatial factors indicates a strong effect of the relative location and distribution of study reaches (e.g., among-site distances, geo-coordinates of the reaches) on fish assemblages. Spatial factors alone can be important predictors of fish assemblages, particularly in highly-modified landscapes where effects such as historic land-cover conversion can limit the apparent influence of current environmental factors (Allan et al. 1997). Overall, shared environmental variables were less influential in our OH catchments, a result also found by Sály et al. (2011) in agricultural catchments in Hungary. In contrast, the relative importance of shared environmental variables in ID suggests that both fish assemblages and environmental conditions were, to some degree, responding to similar driving factors (e.g., ecoregional factors such as underlying geology, topography, and climate). Similarly, Esselman & Allan (2010) found that position within the catchment explained significant variability in fish presence-absence and community measures in Mesoamerican catchments. In both study areas, but particularly in ID, pure environmental (non-spatial) factors accounted for substantial variation in fish assemblage characteristics indicating that assemblages were influenced by environmental variables with no discernible spatial pattern. These non-spatial environmental factors in OH were likely associated with land-use and land-cover changes that are not explicitly constrained by ecoregional characteristics.

**Multi-scale relationships**

The contributions of local- and landscape-scale variables, together with variation explained by the joint influence of both scales, to the overall pure environmental (non-spatial) component were remarkably balanced in our OH study region. In ID, the contribution of local-scale variation to the pure environmental component was predominant. Together, these patterns suggest that the interactions of fish assemblages and their environment are different between our ID and OH study regions. Below, we outline some of these key pure environment-fish patterns, focusing first on the landscape- and subsequently on the local-scale.

At the landscape scale, there was a close positive relationship between species richness and drainage area in both study regions. This association has been well documented for low- to mid-order streams (Sheldon 1968, Oberdorff et al. 1993, Matthews & Robison 1998). In fact, drainage area has been found to be one of the major factors explaining fish species richness in rivers worldwide (Oberdorff et al. 1995). In OH, characterized by high levels of anthropogenic influences on the landscape, factors related to LULC largely constrained fish assemblages. Wang et al. (2003) found similar results in that fish assemblages were more tightly-coupled with broad, catchment-level environmental characteristics in modified landscapes typical of developed areas. Furthermore, Burcher et al. (2007) suggest that catchment LULC likely modifies the hierarchical structure of stream ecosystems to the extent that widespread anthropogenic landscape conversion can reorganize intrinsic fish assemblage structure. Urban development and agricultural LULC are widespread across our OH study region and both have led to considerable modification of hydrological regimes and geomorphic processes, which can negatively influence stream water quality (Johnson et al. 1997, Paul & Meyer 2001, Allan 2004). Even small amounts of impervious surfaces associated with urbanization, for example, can have a disproportionately large, negative impact on stream fish richness and diversity (Allan et al. 1997, Wang et al. 2001).

At the local-scale, we observed that stream habitat and geomorphic condition were important in OH and ID, respectively. Stream habitat assessments integrate a number of influential habitat variables and generally have been found to be closely related to a variety of fish assemblage characteristics (Milner et al. 2006, Sullivan & Watzin 2009). In our study, habitat scores based on the OH QHEI emerged as an important variable aligning most strongly with assemblage density and biomass. Furthermore, we observed a close association between habitat assessment scores and reach-scale geomorphic condition in both study regions. Although geomorphic assessment scores were not significant predictors in the final ordinations for OH, geomorphic condition may also be contributing to reach-level fish descriptors as seen in other studies (e.g., Walters et al. 2003, Sullivan et al. 2006). In general, we also found reaches in better geomorphic condition (e.g., not actively adjusting) and with larger mean sediment size supported greater assemblage diversity, density, and benthic insectivores in the mountain drainage basins in ID. Embeddedness and subsequent declines in benthic habitat heterogeneity, fish assemblage diversity (Berkman & Rabeni 1987), and individual fish condition (Sullivan & Watzin 2010) has been found to be tightly linked to influx of fine sediments to streams. Coarse sediments in mountain streams have also been shown to be especially critical as they are utilized as velocity refuge and cover by many fishes (Fausch 1993).
The relative importance of joint environmental factors suggests that both fish assemblages and local-scale environmental variables were being influenced by similar environmental factors present at broader spatial scales. This pattern points to the interconnectedness between stream fish assemblages and multiple levels of spatial scale. Together with the influence of local-scale factors, this also supports the view that catchments set the upper bounds on environmental and biological characteristics that are spatially nested within them (Frisell 1986, Poff 1997). As spatial position of a stream reach within a drainage network is known to influence fish assemblage properties, this was not an unexpected result (Gorman 1986, Osborne & Schlosser, I. J., 1989: Species area relationships for stream fishes. – Ecology 70: 1450–1462.

Conclusions and future directions

Overall, we observed that in both study regions spatial influences (i.e., pure spatial and spatially-structured environmental influences) accounted for the largest proportion of variation in fish assemblages. When we examined the influence of pure environmental factors (i.e., non-spatial) we observed that fish assemblages were driven by a combination of both broad, landscape-scale as well as local-scale factors. However, fish assemblages were more influenced by local factors in the relatively undisturbed landscapes typical of northern ID. In the highly-developed landscapes typical of OH, human development in the catchment represented the dominant influence on stream fish assemblages, thus providing preliminary evidence related to the potential influence of human activities in restructuring environment-fish relationships. Future research will be needed to fully address multi-scale environmental influences on stream fish assemblages before applications to conservation and management can be made.

The spatial and environmental variables that we used in our ordination analyses accounted for a substantial proportion of assemblage variation. However, the remaining, unexplained portion of variation was likely a result of variables and processes that were beyond the scope of this study. For example, we did not directly incorporate stochastic events such as major floods or point source inputs that may have had acute impact on local fish assemblages in the past and may be reflected in current assemblage composition. Patterns of species dispersal, which can influence the structure of local assemblages (Leibold et al. 2004, Cottenie 2005), were not explicitly modeled in this study but may have also contributed to unexplained variation observed. The greater amount of unexplained variation from our OH catchments may indicate that high-impact human activities on the landscape may introduce additional ‘noise’ into the relationships among the catchment landscape, local habitat, and fish assemblages.

Furthermore, we focused on spatial characteristics that may have links to processes, but we did not explicitly address potential mechanisms. There are myriad challenges associated with linking pattern and mechanism across scales. For example, many processes can operate at scales much larger (or smaller) than they may appear (e.g., pollen dispersal, insect emergence). However, as McIntire & Fajardo (2009) suggest, we may be able to establish precise and unique signatures for spatial processes that we are unable to measure directly. In catchment contexts, this may relate to aquatic-terrestrial exchanges of energy, nutrients, and contaminants (Baxter et al. 2005, Sullivan & Rodewald, in press); linkages between fire pulses and stream food webs (Jackson & Sullivan 2009, Malison & Baxter 2010); and transport and deposition of sediment, both within the channel and across the catchment landscape (Nelson & Booth 2002, Sullivan & Watzin 2010). We anticipate that overtly connecting observed patterns to potential mechanisms will be an important direction of future research and we expect would contribute to an improved understanding of complex, multi-scale ecological relationships in catchment contexts.

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References


Rankin, E. T., 2006: Methods for assessing habitat in flowing waters: using the qualitative habitat evaluation index. – Ohio Environmental Protection Agency, Columbus, OH.


Roth, N. E., Allan, J. D. & Erickson, D. L., 1996: Landscape influences on stream biotic integrity assessed at multiple spatial scales. – Landscape Ecol. 11: 141–156.


Rowe, M., Essig, D. & Jessup, B., 2003: Guide to selection of sediment targets for use in Idaho TMDLs. – Idaho Department of Environmental Quality, Boise, ID.


Shannon, C. E. & Weaver, W., 1949: A mathematical model of communication. – University of Illinois Press, Urbana, IL.


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