A mosaic approach can advance the understanding and conservation of native biodiversity in natural and fragmented riverscapes

by

Sean M. Hitchman

B.S., University of South Carolina, 2004
M.S., University of San Diego, 2011

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2018

Abstract

Understanding the complex relationship between organismal distribution and spatial heterogeneity is central to many ecological questions. This challenge of identifying the biodiversity consequences of spatial patterns is especially critical for resource conservation at the larger riverscape scale because climate- and human-related impacts often act through intricate and spatially-connected organismal-habitat relationships. Specifically, resource managers cannot manage the adverse effects of common disturbances on aquatic ecosystems (e.g. water-withdrawal, dams, urbanization) if the influence of spatial heterogeneity is not recognized and understood. Towards this larger goal, I examined the role of spatial heterogeneity on stream fish biodiversity in the Upper Neosho River, KS in three ways. First, I used a mosaic approach (in which connected, interacting collections of juxtaposed habitat patches were examined) to build the scientific foundation for a general model that aids in the understanding and environmental management of disturbance-related, ecologically-based conservation problems. Second, I examined landscape metrics to quantify the impact of low-head dams on stream habitat and fish diversity. Third, I evaluated multiple quantitative approaches to develop a fuller understanding of how the arrangement of habitats across the riverscape influenced stream fish biodiversity. Related to these questions, the dissertation research provided four key take-home messages that advanced science-based conservation related to stream fish habitat and biodiversity. First, mapping larger-scale patterns of heterogeneity showed that quantitatively-different, physically-distinct pool, riffle, run, and glide habitats were arranged in unique combinations created diverse habitat mosaics across sites. Second, riffles, which comprised < 5% of all habitat patches, acted as keystone habitats that disproportionately increased fish biodiversity (i.e., species richness was significantly higher in mosaics with higher numbers of riffles). Third, mosaic approach metrics

provided new insights into the influence of low-head dams on stream fish biodiversity that were not detected with traditional approaches to habitat sampling and statistical analysis. For example, low-head dams dampened the natural habitat diversity that is needed for the maintenance of resilient communities. Furthermore, using path analysis, I found that species richness was higher immediately below low-head dams as mediated through an increase in the proportion of riffle habitat, but this higher species richness was offset by a greater decrease in species richness in the impoundment habitat above low-head dams. Thus, the choice of scale influenced the interpretation of how dams affected habitat heterogeneity and resultant organismal patterns. Finally, landscape approaches to examining compositional and configurational heterogeneity provided new insights about stream fish habitat-biodiversity relationships. For example, riffle patch density had a positive effect on species richness, species richness was higher within shallow, slow flowing riffles, and adjacent neighbor habitats affected riffle species richness as mediated through alterations to within-habitat characteristics. In summary, quantifying the complex patterns of spatial heterogeneity in a range of ways can aid in the understanding of habitat-biodiversity patterns and help conserve stream fishes at a variety of scales.

A mosaic approach can advance the understanding and conservation of native biodiversity in natural and fragmented riverscapes

by

Sean M. Hitchman

B.S., University of South Carolina, 2004
M.S., University of San Diego, 2011

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2018

Approved by:

Major Professor
Dr. Martha Mather

Copyright

Abstract

Understanding the complex relationship between organismal distribution and spatial heterogeneity is central to many ecological questions. This challenge of identifying the biodiversity consequences of spatial patterns is especially critical for resource conservation at the larger riverscape scale because climate- and human-related impacts often act through intricate and spatially-connected organismal-habitat relationships. Specifically, resource managers cannot manage the adverse effects of common disturbances on aquatic ecosystems (e.g. water-withdrawal, dams, urbanization) if the influence of spatial heterogeneity is not recognized and understood. Towards this larger goal, I examined the role of spatial heterogeneity on stream fish biodiversity in the Upper Neosho River, KS in three ways. First, I used a mosaic approach (in which connected, interacting collections of juxtaposed habitat patches were examined) to build the scientific foundation for a general model that aids in the understanding and environmental management of disturbance-related, ecologically-based conservation problems. Second, I examined landscape metrics to quantify the impact of low-head dams on stream habitat and fish diversity. Third, I evaluated multiple quantitative approaches to develop a fuller understanding of how the arrangement of habitats across the riverscape influenced stream fish biodiversity. Related to these questions, the dissertation research provided four key take-home messages that advanced science-based conservation related to stream fish habitat and biodiversity. First, mapping larger-scale patterns of heterogeneity showed that quantitatively-different, physically-distinct pool, riffle, run, and glide habitats were arranged in unique combinations created diverse habitat mosaics across sites. Second, riffles, which comprised < 5% of all habitat patches, acted as keystone habitats that disproportionately increased fish biodiversity (i.e., species richness was significantly higher in mosaics with higher numbers of riffles). Third, mosaic approach metrics

provided new insights into the influence of low-head dams on stream fish biodiversity that were not detected with traditional approaches to habitat sampling and statistical analysis. For example, low-head dams dampened the natural habitat diversity that is needed for the maintenance of resilient communities. Furthermore, using path analysis, I found that species richness was higher immediately below low-head dams as mediated through an increase in the proportion of riffle habitat, but this higher species richness was offset by a greater decrease in species richness in the impoundment habitat above low-head dams. Thus, the choice of scale influenced the interpretation of how dams affected habitat heterogeneity and resultant organismal patterns. Finally, landscape approaches to examining compositional and configurational heterogeneity provided new insights about stream fish habitat-biodiversity relationships. For example, riffle patch density had a positive effect on species richness, species richness was higher within shallow, slow flowing riffles, and adjacent neighbor habitats affected riffle species richness as mediated through alterations to within-habitat characteristics. In summary, quantifying the complex patterns of spatial heterogeneity in a range of ways can aid in the understanding of habitat-biodiversity patterns and help conserve stream fishes at a variety of scales.

Table of Contents

List of Figures

List of Tables

Acknowledgements

Preface

The contents of this dissertation represent original research developed with my major adviser, Martha Mather, as well numerous other coauthors. As such, Chapters 1, 2, and 3 are presented in the first-person plural and/or third-person in order to facilitate publication in peer-reviewed journals with multiple authors. I list the relevant coauthors for each chapter on the cover page.

Chapter 1 - Identifying keystone habitats with a mosaic approach can improve biodiversity conservation in disturbed ecosystems

Abstract

Conserving native biodiversity in the face of human- and climate-related impacts is a challenging and globally important ecological problem that requires an understanding of spatially-connected, organismal-habitat relationships. Globally, a suite of disturbances (e.g., agriculture, urbanization, climate change) degrades habitats and threatens biodiversity. A mosaic approach (in which connected, interacting collections of juxtaposed habitat patches are examined) provides a scientific foundation for addressing many disturbance-related, ecologically-based conservation problems. For example, if specific habitat types disproportionately increase biodiversity, these keystones should be incorporated into research and management plans. Our sampling of fish biodiversity and aquatic habitat along ten 3-km sites within the Upper Neosho River sub-drainage, KS, from June-August 2013 yielded three generalizable ecological insights. First, specific types of mesohabitat patches (i.e., pool, riffle, run, and glide) were physically distinct and created unique mosaics of mesohabitats that varied across sites. Second, species richness was higher in riffle mesohabitats when mesohabitat size reflected field availability. Furthermore, habitat mosaics that included more riffles had greater habitat diversity and more fish species. Thus, riffles (<5% of sampled area) acted as keystone habitats. Third, additional conceptual development, which we initiate here, can broaden the identification of keystone habitats across ecosystems and further operationalize this concept for

research and conservation. Thus, adopting a mosaic approach can increase scientific understanding of organismal-habitat relationships, maintain natural biodiversity, advance spatial ecology, and facilitate effective conservation of native biodiversity in human-altered ecosystems.

Introduction

Conserving native biodiversity and the habitats that maintain biodiversity is a challenging and globally important ecological problem. Biodiversity provides goods and services to society (Hooper et al., 2005; Maes et al., 2012) and can act as an indicator of ecosystem degradation (Parr et al., 2016). However, human impacts and climate change fragment and degrade habitats in a way that can reduce biodiversity (Fahrig, 2003; Dudgeon et al., 2006; Wilson et al., 2016). The identification of critical habitats that maintain biodiversity is essential to conserve native species and sustain resilient ecosystems. Here, our overarching question is whether specific types of habitats have disproportionate effects on biodiversity (Fig. 1.1). Streams are model ecosystems to develop, define, and refine the keystone habitat concept because they are composed of repeating types of habitat patches, which individually and collectively can drive the distribution and abundance of stream biota (i.e., pool, riffle, run, glide mesohabitats; Frissell et al., 1986; Newson & Newson, 2000).

Freshwater ecosystems are among the most imperiled ecosystems worldwide. A suite of anthropogenic disturbances (Dudgeon et al., 2006; Vörösmarty et al., 2010; Matono et al., 2014) exacerbated by climate change (e.g., Almodovar et al., 2012; Hauer et al., 2013; Floury et al., 2013) alters hydrology, modifies aquatic habitats, and threatens freshwater biodiversity. Globally, species are declining at higher rates in freshwater ecosystems than terrestrial and marine systems (Dudgeon et al., 2006; Vaughn, 2010). For example, the proportion of North

American freshwater fishes that are imperiled or extinct has increased by 40% over the last 20 years (Jelks et al., 2008). The distribution of organisms and overall biodiversity in streams are strongly influenced by habitat (Smith & Mather, 2013; Silva et al., 2014). Therefore, it is critical to identify and conserve the habitats that promote biodiversity in these and other threatened ecosystems.

Here we seek to develop, define, and refine the keystone habitat concept using fish biodiversity in a stream ecosystem. Several approaches have been used to examine organismal-habitat relationships. We used a mosaic approach to develop the keystone habitat concept since this approach explicitly considers habitat composition (e.g., number and relative amount of each habitat type; Li & Reynolds, 1995; Malard et al., 2002; Barnes et al., 2013). The mosaic approach views ecosystems as a collection of physically distinct habitat units (Pringle et al., 1988; Winemiller et al., 2010; Kleindl et al., 2015). As a result, this approach allows for the quantification of the relative proportion of mesohabitat patches across the landscape, which in turn facilitates an examination of interactions among habitat patches. Although mosaics include commonly studied habitat types, here we test if new ecological metrics, properties, and insights emerge from examining these connected, interacting collections of juxtaposed habitat types. A second approach to organismal-habitat relationships relates a range of habitat variables to organismal distribution and diversity at individual sites, often along equally spaced transects (Didham et al., 1998; Stefanescu et al., 2004; Kwik & Yeo, 2015). However, these spatially-isolated, small-scale data typically do not accurately predict patterns of biotic changes at larger scales or in response to major disturbances. A third approach to organismal-habitat relationships characterizes habitat using intermediate-scale geomorphological habitat patches (Taylor, 2000; Schwartz et al., 2015). This approach has been useful in identifying organismal-habitat

relationships (Kruess, 2003; Erös, 2007; Naskar et al., 2015), but viewing mesohabitats as separate, isolated units often results in low resolution for detecting site-to-site variation. Although less common, the mosaic approach, which we use here, has advantages over transect and geomorphic approaches and is applicable to an array of aquatic and terrestrial ecosystems (Bulleri & Benedetti-Cecchi, 2006; Williams & Kremen, 2007; Villemey et al., 2015).

The keystone concept has been widely applied to species (e.g., Paine, 1969; Delibes-Mateos et al., 2011; Mouquet et al., 2013). For example, a Web of Science search yielded over 1,100 journal articles on "keystone species" published from 1980 to 2016, including 91 with > 100 citations. Since the reporting of the dramatic changes in a rocky intertidal community that occurred with the removal of a predatory starfish (Pisaster ochraceus; Paine, 1966; cited 2,898 times), the keystone species concept has been refined to describe a species that has a disproportionately large effect on its community or ecosystem relative to its abundance (e.g., Power et al., 1996). Well-documented cases of keystone species include sea otters in kelp forests (e.g., Estes & Palmisano, 1974; Estes & Duggins, 1995; Kenner et al., 2013), trophic cascades in lakes and oceans (e.g., Carpenter et al., 1985; Carpenter & Kitchell, 1988; Hessen & Kaartvedt, 2014), and fish in streams (e.g., Power et al., 1985; Schindler et al., 1997; Small et al., 2011). The keystone species concept has been expanded from top predators to prey species (Holt, 1977; Utne-Palm et al., 2010), parasites (Evans et al., 2011; Roche et al., 2013), mutualists (Gilbert, 1980; Betts et al., 2015), and ecosystem engineers (Naiman et al., 1986, Jones et al., 1994, Magle & Angeloni, 2011). Recently, a variety of quantitative approaches (e.g. community viability analysis, community sensitivity analysis, ecological network analysis) have been used to measure interaction strength and to understand community importance (e.g., Berg et al., 2011; Aizen et al., 2012, Stouffer et al., 2012). Functional importance (Hurlbert, 1997; Davic, 2003)

and unique roles (Kotliar, 2000) have been emphasized to address the criticism that the keystone species concept has become too broad to be useful (Strong, 1992; Mills et al., 1993; Cottee-Jones & Whittaker, 2012). Keystone species have an exceptional ability to influence biodiversity. However, the ability to predict the presence and strength of keystone species a priori is limited in that context affects the "quest for keystones" (Power et al., 1996).

In contrast, the keystone concept has rarely been applied to habitat (Davidar et al., 2001; Bonnet et al., 2009). At smaller spatial scales, the term 'keystone structure' has been used to describe structures that provide goods and services to maintain species diversity (Tews et al., 2004). At a regional scale, Davidar et al. (2001), while investigating bird species richness in the presence of wet forests in the Andaman Islands, used the term keystone habitat to describe habitat that maintains biodiversity. The keystone habitat concept could apply to a range of ecosystems: (a) if a more specific definition existed to determine the types of habitat that can be considered keystones, (b) if better details on the linkage between habitat and biodiversity were available, and (c) if a framework was developed to generalize the impact of keystone habitats across organisms and ecosystems.

To develop the keystone habitat concept in a way that can improve conservation planning and outcomes in the face of global change, we asked five specific research questions (Fig. 1.1). First, are mesohabitat patches (i.e., pool, riffle, run, and glide) statistically distinct based on physical variables (i.e. depth, width, water velocity, and substrate)? In many ecosystems, discrete habitats do not exist because physical variables change along a continuous gradient. However, here we predict that stream habitat categories will vary predictably in physical features. Second, do the number and type of habitat patches within each distinct mesohabitat type vary across mosaics? In some ecosystems with homogeneous habitat, mosaics may not exist or may be too

simple or rare to be functionally important. Alternatively, here we predict that mosaics can vary in composition and configuration throughout the watershed. Third, does biodiversity differ among individual stream mesohabitat patches? We predict that distinct relationships persist between mesohabitat type and fish biodiversity. Fourth, using the mosaic approach, do keystone habitats (i.e., habitats that affect biodiversity disproportionately relative to their abundance) exist? Habitat patches could influence biodiversity independent of other habitat types that surround them. Alternatively, mesohabitat patches could interact with surrounding habitats to produce effects on biodiversity that would be overlooked if habitat patches were examined in isolation. Finally, can the predictions and insights from the keystone species concept, developed using food web ecology, inform the keystone habitat concept or do the two keystone concepts function in fundamentally different ways?

Materials and Methods

Study Area

The Neosho River drainage joins the Arkansas River in northeastern Oklahoma (Juracek & Perry, 2005; Fig. 1.2a). Our study area, the Upper Neosho River sub-drainage, includes the 5th order (Strahler, 1957) Cottonwood and Upper Neosho Rivers and drains approximately 7,770 km2 upstream of the John Redmond Reservoir (Fig. 1.2b). The Upper Neosho and Cottonwood Rivers lie predominantly on Permian age limestone and shale bedrock overlain by Quaternary alluvium (Juracek & Perry, 2005). Land use is dominated by agricultural fields of soybean, wheat, and corn with small riparian zones adjacent to the crop fields and streams (Tiemann et al., 2004). The Neosho River contains a diverse native fish fauna of 55 species (Cross, 1967) that are

adapted to longitudinally-connected, predictably-variable flow and temperature regimes (Dodds et al., 2004).

In order to identify keystone habitats, we examined fish biodiversity-habitat patterns in the Upper Neosho River sub-drainage. Our research focused on adjacent mesohabitat patches (pool, riffle, run, and glide) at ten 3-km sites. Six sites (Sites 1-6) were located along the Upper Neosho River (Fig. 1.2b). One site (Site 7) was located just below the confluence of the Upper Neosho and Cottonwood Rivers, and three sites (Sites 8-10) were located on the Cottonwood River (Fig. 1.2b). This project was undertaken in conjunction with a larger project that investigated potential impacts of low-head dams on the native stream fish community. Consequently, we sampled fish and habitat at five sites below low-head dams (Sites 1, 4, 5, 8, 10, Fig. 1.2b) and five sites located at undammed locations (Sites 2, 3, 6, 7, 9, Fig. 1.2b). All intact low-head dams in the upper Neosho River drainage [< 3 m height, constructed in 1860-1995, for milling, water supply, recreation (Fencl et al., 2015)] were sampled. Undammed sites were selected based upon distance from dam sites, stream accessibility, and landowner permission. Sampling was identical at dammed and undammed sites (see below). Because no direct and consistent statistical differences in habitat (number of patches per mesohabitat type) existed between dammed and undammed sites (W = 17, p = 0.42; Wilcoxon rank sum test), all sites were analyzed together. The Upper Neosho River sub-drainage is a stream network that has the potential to provide general insights for understanding human impacts and climate change in streams for diverse geographic regions. Streams in the Great Plains have a naturally variable hydrologic regime characterized by regularly occurring floods and droughts (Dodds et al., 2004). Mean annual discharge at our study sites were 8.72 m3s-1 (SE± 0.94, USGS gage 07179730,

1963-2013) and 24.55 m3s-1(SE± 2.19, USGS gage 07182250, 1963-2013) for the Neosho and Cottonwood Rivers, respectively.

Mesohabitat Patch Characteristics

Environmental variables (i.e., wetted stream width, water depth, water velocity, and median substrate size) were measured at 20 randomly selected habitat patches (five in each of our four mesohabitat types) at each of our ten 3-km sites (Fig. 1.2b). If there were less than five patches of a particular mesohabitat type at a sample site, all patches of that mesohabitat type were sampled. The four major mesohabitat patches that we quantified in our study system were pools, riffles, runs, and glides. These channel units are described in detail elsewhere (McCain et al., 1990; Hawkins et al., 1993; Bisson et al., 2006). Pools have slow, deep, non-turbulent flow with fine substrate. Riffles have fast, shallow, turbulent flow in which the stream substrate breaks the surface. Runs (fast, non-turbulent flow, deeper than riffles) and glides (slow, non-turbulent flow, shallower than pools) are intermediate in physical features. Wetted stream width was recorded using a Nikon 8398 range finder (<1 m accuracy, range 3-200 m) at the midpoint of each mesohabitat patch. At five equally-spaced sampling points along the cross-stream transect, water depth, water velocity, and median substrate sizes were quantified. Depth (m) was measured with a meter stick. Flow velocity (60% of the depth) was measured with a Marsh-McBirney Model 2000 flowmeter. Substratum was classified using a modified Wentworth scale (Wentworth, 1922) ranging from 0 to 6 (0 = clay, 1 = silt, 2 = sand, 3 = gravel, 4 = pebble, 5 = cobble, 6 = boulder). A stepwise discriminant function analysis was used to evaluate if the mesohabitat patch types were distinct based on water depth, water velocity, and mean substrate size. Width was not included in the discriminant function analysis due to multicollinearity with

water depth. Environmental variables were log-transformed to satisfy statistical assumptions. A chi-square approximation of Wilks' lambda (Manly, 1986) was used to evaluate the separation among mesohabitat patch types. A jackknife cross-validation procedure assessed accuracy in assigning mesohabitat patch types, based upon the environmental variables (MASS package; Venables & Ripley, 2002).

Mesohabitat Patch Distribution and Proportion

We mapped interacting sequences of mesohabitat patches within each of our ten 3-km sampling sites to examine if discrete mesohabitat patches formed habitat mosaics that varied across sites. Sampling occurred during baseflow conditions (13.0-19.0 m3s-1; USGS gage 07182250). During June-August, 2013, while kayaking downstream, we identified, measured and mapped the incidence and locations of mesohabitat patches based on agreement by two independent observers using an objective series of surface flow, channel morphology, and sediment composition criteria (McCain et al., 1990; Harvey & Clifford, 2009).

We quantified size and location of mesohabitat patches by using trackplots at 5-s intervals and waypoints at the upper and lower boundary for each habitat unit from a handheld Garmin GPSmap76Cx (Garmin International, Olathe, KS). Trackplots and waypoints for each sample site were imported into ArcMap v. 10.2 (ESRI, Redlands, CA). Mesohabitat patches at each site were digitized into polygons in ArcMap 10 and stored as separate feature classes in the geodatabase. Each polygon layer was converted to raster format to visualize habitat for each of the sample sites.

Fish Biodiversity-Sampling

To quantify fish biodiversity, we captured fish using a two- person mini-Missouri trawl. In multiple and diverse publications from 2009-2016, the mini- Missouri trawl has been used to capture both small (Herzog et al., 2009; Driver & Adams, 2013) and large-bodied (Hintz et al., 2016) fish across a variety of aquatic ecosystems including streams and large rivers (Harrison et al., 2014; Starks et al., 2015), lakes and impoundments (Fischer & Quist, 2014; Pratt et al., 2016), coastal plains (Kirk et al., 2010) and island complexes (Hintz et al., 2015). The mini-Missouri trawl is a two-seam slingshot balloon trawl covered with a 3.2 mm delta style mesh that can be used in wadeable and non-wadeable areas of the river (Herzog et al., 2009). We chose this gear to ensure consistent sampling across mesohabitats and study sites. In a gear experiment in the Neosho River, we found that the mini-Missouri trawl caught as many or more species than other common fish sampling gear (mini-Missouri trawl = 7 species, seine = 6 species; hoop nets = 6 species; backpack electrofisher = 4 species; Fencl personal communication). Within each mesohabitat patch that we sampled, two people pulled the trawl through a standard 30 m transect from upstream to downstream at a speed slightly faster than the current speed, as is advocated by the gear developers (Herzog et al., 2009). Captured fish were placed in an aerated live well, identified to species, enumerated, and then returned alive to the stream. We measured α diversity (Whittaker, 1972) in up to 5 of each type of mesohabitat at each sample site. Traditionally α diversity is measured at the site (or reach) scale and not broken into habitat components within a stream. Measuring α diversity within each mesohabitat allowed us to determine if keystone mesohabitats existed.

Fish-Mesohabitat Relationships

We used non-metric multidimensional scaling (NMDS) on two fish datasets, (abundance and presence-absence) to quantify species-habitat relationships within mesohabitats. In the abundance dataset, common species were dominant, whereas for presence-absence data, all species had equal influence (Legendre & Legendre, 1998). NMDS has been shown to be a robust technique for analyzing ecological data (Minchin, 1987) and has been used elsewhere to analyze distribution patterns (e.g., Heino et al., 2002; Kiernan et al., 2012). For the NMDS, we used a Bray-Curtis distance matrix that quantified the similarity among patches for which mesohabitat type was the factor (row) and fish assemblage (species abundance, species presence-absence) was the response variable (column). Data represented a standard 30 m sample. Separation for the species assemblage associated with each mesohabitat type was analyzed using analysis of similarity (ANOSIM) in which a p value < 0.05 indicated a unique species assemblage associated with a particular mesohabitat type. We used the metaMDS function (distance = bray) under package vegan in R (Oksanen et al., 2013).

Identifying Keystone Habitats

We compared biodiversity patterns between isolated mesohabitats and mosaics (combinations of adjacent, connected interacting mesohabitats) using multiple graphic and statistical analyses. For these analyses, we imported the raster files of the habitat maps for each sample site into FRAGSTATS 4.1 (McGarigal et al., 2012). First, to assess if any mesohabitat type in our study area was limiting, we created barplots of the proportion of each mesohabitat type and mean patch size across sample sites. Second, to evaluate the effect of mesohabitat type on fish diversity, we compared mean species richness (aggregated by all species captured within

a particular mesohabitat type across all sample sites) for each mesohabitat type. Alternatively, to test if any mesohabitat type had a disproportionate effect on species richness (i.e., were keystone habitats) when availability of mesohabitats reflected natural field conditions, we created barplots of weighted species richness for each mesohabitat type (mean species richness within a mesohabitat shown in proportion to the availability of each mesohabitat across sample sites). Species richness-mesohabitat comparisons were analyzed using Kruskal-Wallis nonparametric tests for which mesohabitat type was the treatment and species richness was the response.

Third, to quantify the role of mesohabitat patches within the mosaic (i.e., examining all mesohabitats combined rather than individual mesohabitats patches separately), we ran additional analyses. We used linear regression to test if habitat diversity (Shannon's habitat diversity = regressor) affected mosaic species richness (response). We also ran four additional linear regressions to examine the effect of mesohabitat density (number of pools, riffles, runs, and glides per km2, respectively = regressors) on mosaic species richness (response). Finally, using multiple regression, we assessed the relative role of each mesohabitat using multimodel inference (AICc; Burnham and Anderson 2003) and the "glmulti" package in R (Calcagno, 2013). For this last analysis, mosaic habitat heterogeneity and species richness were the response variables in two separate AICc analyses for which multiple regressors were patch densities of each of the four mesohabitat types. All possible combinations of regressors were included as candidate models. From these multiple regressions, we calculated model-averaged slope (β), a measure of effect size, and variable importance. If a single mesohabitat is more influential in the mosaic, the corresponding average slope and variable importance will be large compared to the other mesohabitats. For all analyses, statistical assumptions were tested. All analyses were performed using R (R Development Core Team, 2013).

Results

Mesohabitat Characteristics

Mesohabitat categories, based on a multivariate combination of depth, water velocity, and mean substrate size, were quantitatively distinct (Fig. 1.3a). The first and second discriminant functions accounted for 93.9% and 4.9% of the total variance associated with mesohabitat group dispersion, respectively (Fig. 1.3a). A low Wilks' Lambda value ($\lambda = 0.09$, $p < 0.001$) indicated that our three mesohabitat-specific environmental variables effectively discriminated among riffle, run, pool, and glide mesohabitat categories. In a cross-validation of jackknifed mesohabitat-environmental variable scores, 87% of all mesohabitats were classified correctly. Pools were characterized by deep, slow-flowing water with relatively fine substrate (Fig. 1.3b). Riffles were the shallowest and fastest mesohabitats with the coarsest substrate (Fig. 1.3b). Runs had shallower intermediate depths with fast-flowing waters (Fig. 1.3b) whereas glides had deeper intermediate depths with slow-flowing water (Fig. 1.3b).

Mesohabitat Distribution and Proportion

The number and type of mesohabitat patches varied across all ten 3-km sample sites (Fig. 1.4a-j, Sites 1-10). The total number of patches per 3-km ranged from 17 (Fig. 1.4j, Site 10) to 59 (Fig. 1.4b, Site 2). Riffle (mean = 6.3, range = 3-9 patches per site), and run mesohabitats (mean = 8.1, range = 2-16 patches per site) were present across all sites. In the Neosho River, glides (mean = 6.5, range = 0-18 patches per site) were an irregularly distributed (absent at 30% of sites) transitional habitat associated with riffles or pools (adjacent to pools 68-74%; adjacent to riffles 19-21%). The composition of stream mesohabitat varied across sites. Habitat diversity

(Shannon's habitat diversity index) ranged from 0.85 to 1.53. The abundance of habitat types at each sample site differed ($\chi^2 = 70.42$, $p < 0.001$). The number of patches at dammed sites ranged from 17 (Fig. 1.4j, Site 10) to 40 (Fig. 1.4a, Site 1) and the number of patches at undammed sites varied from 19 (Fig. 1.4g, Site 7) to 59 (Fig. 1.4b, Site 2). Thus, mesohabitat patch combinations were variable at sites both with (Fig. 1.4a, d, e, h, j; Sites 1, 4, 5, 8, 10) and without dams (Fig. 1.4b, c, f, g, i, Sites 2, 3, 6, 7, 9). Mesohabitats were not consistently different between dammed and undammed sites (W = 17, $p = 0.42$).

Fish-Mesohabitat Relationships

We sampled a total of 7,791 fish representing 35 species across seven families at ten sites within the Upper Neosho River sub-drainage (Table A.1). Based on NMDS analyses, fish assemblages differed among mesohabitats for abundance (ANOSIM Global R = 0.24, $p < 0.001$; Fig. 1.5a) and presence absence datasets (ANOSIM Global R = 0.20, $p < 0.001$; Fig. 1.5b). The separation was greatest between riffles and other mesohabitats for both biodiversity datasets (Fig. 1.5). Specifically, riffles contained more species and more individuals that were riffle specialists (Central Stoneroller, Suckermouth Minnow; Table B.1, Fig. B.1), riffle generalists (Bluntnose Minnow Table B.1, Fig. B.1), riffle-run generalists Shiner (Red Shiner, Bluntface Shiner Table B.1, Fig. B.1), and generalists (Slenderhead Darter Table B.1, Fig. B.1).

Identifying Keystone Habitats

Proportionally by area, pools were the most common mesohabitat and riffles were the least common mesohabitat across all sample sites ($\chi^2 = 20.6$, $p < 0.001$; Fig. 1.6a). Based on surface area, pools were also the largest mesohabitat, and, in general, were an order of magnitude

14

larger than riffles, runs, and glides ($\chi2 = 20.6$, $p < 0.001$; Fig. 1.6b). Mean species richness was not different for standard 30-m samples across mesohabitats ($\chi2 = 1.23$, $p = 0.54$; Fig. 1.7a). However, when mean species richness was weighted by field mesohabitat availability, species richness was significantly higher in the riffle mesohabitat ($\chi2 = 5.15$, $p < 0.001$; multiple comparison: riffle > run, glide > pool; $p < 0.05$; Fig. 1.7b).

For the entire suite of habitats at each of our sample sites (i.e., the mosaic), a significant, positive relationship existed between habitat diversity and species richness ($r^2 = 0.70$; $p < 0.01$; Fig. 1.8a). In univariate regressions, species richness increased with riffle patch density ($r^2 = 0.47$; $p = 0.03$; Fig. 1.8b) and to a lesser degree with glide patch density ($r^2 = 0.39$; $p = 0.07$; Fig. 1.8e). However, species richness did not increase with pool patch density (Fig. 1.8c) or run patch density (Fig. 1.8d).

When the relative roles of individual mesohabitats were evaluated using multimodel inference, of all mesohabitats present within mosaics, riffles had the largest effect on habitat diversity (model averaged slope = 0.08; Fig. 1.9a) and species richness (model averaged slope = 2.12, Fig. 1.9b). In both AICc analyses, variable importance was also much greater for riffles compared to other mesohabitats for habitat heterogeneity (riffles = 0.42, glides = 0.26, runs = 0.07, pools = 0.13) and species richness (riffles = 0.55, glides = 0.28, runs = 0.09, pools = 0.09).

Discussion

Our approach to understanding biodiversity-habitat relationships in spatially-connected ecosystems can increase the effectiveness of conservation in human-altered ecosystems. Several important take-home messages emerged from our research. First, combinations of environmental variables created discrete mesohabitat patches that formed varying patterns of connected mosaics

across the riverscape. This quantifiable physical template provided the structural foundation for the keystone habitat concept. Second, riffles functioned as keystone habitats because habitat mosaics that contained more riffle patches had disproportionally greater biodiversity. The mosaic approach was essential for detecting riverscape patterns. If we had not used this approach, which considered the arrangement and connections as well as the type and amount of mesohabitats, we would not have detected these patterns. Third, keystones (species versus habitats) share features but differ in organization and hierarchy. Consequently, a new conceptual framework, as we initiated here, is needed to advance the keystone habitat concept. Considered together, the insights from our research show that the keystone habitat concept can help researchers and environmental practitioners understand and manage responses to global change in human-altered ecosystems. Specifically, this underutilized concept can guide future research in spatial ecology, clarify how anthropogenic and climate disturbances affect biodiversity through habitat, and inform conservation. These take-home messages are discussed in detail below.

Discrete Habitat Patches Create Mosaics

For keystone habitats to exist, the landscape must include discrete habitat units (Forman and Godron, 1986; Turner et al., 2001). Mesohabitat types in our study were quantitatively separate based on variation in water depth, water velocity, and mean substrate size. Pool, riffle, and run mesohabitats are commonly used to classify stream habitats in other lotic systems across ecoregions (Hynes, 1970; Frissell et al., 1986; Hauer et al., 2011) and have been shown to be ecologically meaningful (Matthews et al., 1994; Schwartz & Herricks, 2008; Naskar et al., 2015). Of course, natural habitats have also been quantified using continuous variables. However, our mesohabitats varied along continuous variables, pool, riffle, run, and glide were

categorically distinct in our system. Although differences existed in fish assemblages across all mesohabitats, our NMDS analysis showed that riffle assemblages were the most distinct. The use of distinct and discrete habitat patches paves the way for a while series of innovative conceptual frameworks such as we develop below.

Riverscape Patterns Would Not Have Been Detected Without the Mosaic Approach

The mosaic approach allowed us to quantify the structure and function of keystone habitats. For example, when an individual habitat type has a greater effect on biodiversity than other habitat types because it interacts with the habitats surrounding it (e.g., creates habitat heterogeneity), then examination of habitat patches without consideration of surrounding habitats will misrepresent the overall effect of that habitat type. The majority of fish habitat studies have considered mesohabitats as separate, individual habitat types (Schlosser, 1982). Because the composition and configuration of patches affects biological patterns and processes (Pringle et al., 1988; Lowe et al., 2006; Pichon et al., 2015), examining mesohabitat patches in the context of how they create mosaics of habitat across the landscape is essential. Mapping adjacent habitat patches across the landscape and linking community assemblage structure within and among patches is an important step to identifying keystone habitats.

Riffles Were Keystone Habitats

In the Neosho River, riffles acted as a keystone habitat by disproportionately influencing fish species richness within collections of adjacent and interacting mesohabitats. Riffles constituted the least amount of available habitat in the study area. However, within mosaics, species richness was greater at sites with a higher density (# per km2) of riffles. Although glides influenced habitat heterogeneity in univariate regressions, multimodel inference on multiple

regression models showed that riffles were the dominant mesohabitat responsible for increased mosaic habitat diversity and species richness [i.e., larger effect sizes (slope) and larger variable importance compared to all other mesohabitat types].

The higher overall species richness at locations with a higher density of riffles was not simply related to (a) the presence of more riffle species because species richness was not different across standard samples of individual mesohabitat types (pool, riffle, run, and glide), (b) a species-area relationship because riffle mesohabitat constituted the smallest and least common mesohabitat, by area, along the Neosho and Cottonwood Rivers, or (c) simply adding more habitats because an increase in run and pool patches did not yield the same increase in species richness. Riffles are prominent features in prairie streams (e.g., well oxygenated environments; Greig et al., 2007) that provide functions not found in other habitats. These functions include specialized spawning and rearing habitat for many fish species (Teichert et al., 2013) or refuges from fish predation (Schlosser, 1987). We speculate that these unique functions of riffles attract specialists, generalists, and other fish moving among mesohabitats.

Keystone Species vs. Keystone Habitats

At least three aspects of the well-developed keystone species literature could be directly transferable to the keystone habitat concept. First, using previous operational definitions of the keystone species concept (Power et al., 1996; Kotliar, 2000), we propose a detailed definition of a keystone habitat with the following hallmarks: 1) keystone habitats have a large effect on community structure (e.g. species richness), 2) the effects of keystone habitats are large relative to their availability, and 3) keystone habitats provide a function not performed by other available habitats. Second, keystone species traits are not ubiquitous across space and time (Mills et al.,

1993; Menge et al., 1994) and keystone species are inherently context dependent (Christianou &

Ebenman, 2005; Cottee-Jones & Whittaker, 2012). Likewise, complexity likely exists in

widespread generalizations about keystone habitats. Third, consequences of both keystone

concepts are substantial, in that both food webs with keystone species and landscapes with

keystone habitats function differently than those without keystones. Neither food webs nor

habitats can be understood, maintained, restored, or conserved without considering keystones.

Keystones for species and habitats may be quite different, however, suggesting that many

predictions about keystone species may not be directly applicable to keystone habitats. Species

within a food web are linked in predictable ways relative to trophic role. As examples, predators

have a clear hierarchical top-down connection to their prey, shared resources define the lateral

position of competitors in a food web, and trophic position (via diets and isotopes) is the

common currency for creating food webs. These energetic links impose an order on species

within food webs that is the basis for much food web theory (e.g., food chain length). In contrast,

we know very little about conceptual, functional, and geographic links that connect physical

habitat types and fish communities across habitats. At present, a conceptual structure (network,

web, or other) that applies to the composition and function of habitats across landscapes is

lacking. Without this basic information on how habitat patches are functionally connected, many

predictions about keystone species from food web theory are difficult to directly apply to

keystone habitats.

Conservation Benefits

Identifying keystone habitats is relevant to the understanding, conservation and

restoration of biodiversity in disturbed ecosystems in that human and climate disturbances alter

habitats. Rivers are highly dynamic ecosystems consisting of a suite of habitat types, likely promoting resilience among aquatic communities under changing conditions. Human impacts (e.g., agriculture and urbanization) and climate change (IPCC, 2013) are predicted to alter some combination of water withdrawal, precipitation, and land use. As a result, these ubiquitous disturbances will alter the flow regime causing increased floods (Pall et al., 2011), increased droughts (Mishra et al., 2010; Cooke et al., 2015), decreased natural flow variation, and decreased hydrologic connectivity (Jaeger et al., 2014; Castello and Macedo, 2016). Climate change models for the U.S. Great Plains predict that more intense precipitation events will deliver the same amount of rainfall in a shorter time period (Meehl et al., 2005; Christensen et al., 2007), resulting in more extreme floods and longer droughts (IPCC, 2013). In the Neosho River, riffles promote higher habitat heterogeneity and maintain biodiversity. However, with more intense precipitation expected as a result of climate change (Meehl et al., 2005; Christensen et al., 2007), the hydrologic regime will be altered (e.g. extreme droughts and floods). Drought reduces overall habitat area, disconnects floodplain and mainstem habitats, limits access to critical spawning and refuge habitats by fragmentation (Stanley et al., 1997; Magoulick & Kobza, 2003; Jaeger et al., 2014), and can alter functional community structure (Boucek & Rehage, 2014). Riffles are typically the first instream habitats to dewater during hydrologic drought. For example, a 1999 drought in West Virginia headwater streams caused a 96% reduction in stream discharge, a 52% reduction of riffle habitat area, but only a 2% reduction in pool habitat area (Hakala & Hartman, 2004). Not only do the impacts of hydrologic drought negatively impact the abundance and growth of riffle-dwelling species (Avery-Gomm et al., 2014), but this extreme drying fragments the riverscape, resulting in a decrease in overall biodiversity (Lake, 2003). At the other extreme of disturbance, periods of intense precipitation

are expected to increase discharge, raise water levels, and also eliminate riffle habitat through flooding (de Almeida et al., 2011). Keystone habitats, identified through a mosaic approach, provide a scientific foundation for addressing these disturbance-related, global conservation problems (agriculture, urbanization, water withdrawal, and climate).

Summary

The mosaic approach and keystone habitat concept could have broad generality to other organisms and ecosystems through the implementation of relatively simple conceptual and empirical extensions. Many organisms use multiple habitats (Law & Dickman, 1998; Dahlgren & Eggleston, 2000; Rosenberger & Angermeier, 2003). These specific habitats serve different functions such as spawning or nesting habitats (Isaak et al., 2007; Hagen et al., 2013), nursery habitats (Barceló et al., 2016), movement corridors (Machtans et al., 1996; Blåzquez-Cabrera et al., 2016) or biogeochemical hotspots (McClain et al., 2003; Lautz & Fanelli, 2008; Bernhardt et al., 2017). Future research that examines both if these individual habitats function differently, whether some habitats may be disproportionally important, and if the arrangement of habitats changes the ecological outcome can advance both science and conservation.

Only a few examples of keystone habitats exist at present, but here, we have initiated a framework that can expand the keystone habitat concept to other ecosystems. For example, our approach outlines how to identify critical habitat that maintains biodiversity: (1) evaluate whether individual habitat patches are unique and discrete physical entities, (2) demonstrate through habitat surveys that individual mesohabitats create clear and diverse mosaics of habitat along the stream channel, (3) assess habitat-biodiversity relationships for individual habitat patches, and (4) compare biodiversity patterns in individual mesohabitats to integrated habitat

mosaics. Identifying the distribution, arrangement, and function of habitat patches across a wide collection of landscapes is the next step in the development of the keystone habitat concept for other ecosystems. Consequently, evaluating biodiversity response to the habitat mosaic can add a new dimension to spatial ecology and increase the effectiveness of conservation in a range of ecosystems impacted by global changes.

References

Aizen MA, Sabatino M, Tylianakis JM (2012) Specialization and rarity predict nonrandom loss of interactions from mutualist networks. Science, **335**, 1486–1489.

Almodovar A, Nicola GG, Ayllon D, Elvira B (2012) Global warming threatens the persistence of Mediterranean brown trout. Global Change Biology, **18**, 1549-1560.

Avery-Gomm S, Rosenfeld JS, Richardson JS, Pearson M (2014) Hydrological drought and the role of refugia in an endangered riffle-dwelling fish, Nooksack dace (*Rhinichthys cataractae ssp.*). Canadian Journal of Fisheries and Aquatic Sciences, **71**, 1625-1634.

Barceló C, Ciannelli L, Olson EM, Johannessen T (2016) Eight decades of sampling reveal a contemporary novel fish assemblage in coastal nursery habitats. Global Change Biology, **22**, 1155-1167.

Barnes JB, Vaughan IP, Ormerod SJ (2013) Reappraising the effects of habitat structure on river macroinvertebrates. Freshwater Biology, **58**, 2154-2167.

Berg S, Christianou M, Jonsson T, Ebenman B (2011) Using sensitivity analysis to identify keystone species and keystone links in size-based food webs. Oikos, **120**, 510-519.

Bernhardt ES, Blaszczak JR, Ficken CD, Fork ML, Kaiser KE, Seybold EC (2017) Control points in ecosystems: Moving beyond the hotspot hot moment concept. Ecosystems, doi:10.1007/s10021-016-0103-y.

Betts MG, Hadley AS, Kress WJ (2015) Pollinator recognition by a keystone tropical plant. Proceedings of the National Academy of Sciences of the United States of America, **112**, 3433-3438.

Bisson PA, Buffington JM, Montgomery DR (2006) Valley segments, stream reaches and channel units. In: Methods in Stream Ecology (eds Hauer FR, Lamberti GA) pp. 23-49,

Elsevier, San Diego.

Blåzquez-Cabrera S, Gastón A, Beier P, Garrote G, Simón MA, Saura S (2016) Influence of separating home range and dispersal movements on characterizing corridors and effective distances. Landscape Ecology, **31**, 2355-2366.

Bonnet X, Brischoux F, Pearson D, Rivalan P (2009) Beach rock as a keystone habitat for amphibious sea snakes. Environmental Conservation, **36**, 62-70.

Boucek RE, Rehage JS (2014) Climate extremes drive changes in functional community structure. Global Change Biology, **20**, 1821-1831.

Bulleri B, Benedetti-Cecchi L (2006) Mechanisms of recovery and resilience of different components of mosaics of habitats on shallow rocky reefs. Oecologia, **149**, 482-492.

Calcagno V (2013). glmulti: Model selection and multimodel inference made easy. R package version 1.0.7. https://CRAN.R-project.org/package=glmulti

Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. Bioscience, **35**, 634-639.

Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. Bioscience, **35**, 764-769.

Castello L, Macedo MN. 2016. Large-scale degradation of Amazonian freshwater ecosystems. Global Change Biology 22: 990-1007.

Christensen JH, Hewitson B, Busuioc A *et al.* (2007) Regional climate projections. Climate Change, 2007: The Physical Science Basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, University Press, Cambridge, Chapter 11, 847-940.

Christianou M, Ebenman B (2005) Keystone species and vulnerable species in ecological

communities: strong or weak interactors? Journal of Theoretical Biology, **235**, 95–103.

Cooke BI, Ault TR, Smerdon JE (2015) Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances, **1**, e1400082.

Cottee-Jones HEW, Whittaker RJ (2012) The keystone species concept: A critical appraisal. Frontiers of Biogeography. **4.3**, 117-124.

Cross FB (1967) Handbook of fishes of Kansas. University of Kansas, Natural History Museum.

Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology, **81**, 2227-2240.

Davic RD (2003) Linking keystone species and functional groups: A new operational definition of the keystone species concept. Conservation Ecology, **7**, URL: http://www.consecol.org/vol7/iss1/resp11/.

Davidar P, Yoganand K, Ganesh T (2001) Distribution of forest birds in the Andaman islands: Importance of key habitats. Journal of Biogeography, **28**, 663-671.

de Almeida GM, Rodriguez JF (2011) Understanding pool-riffle dynamics through continuous morphological simulations. Water Resources Research, **47**.

Delibes-Mateos M, Smith AT, Slobodchikoff CN, Swenson JE (2011) The paradox of keystone species persecuted as pests: A call for the conservation of abundant small mammals in their native range. Biological Conservation, **114**, 1335–1346.

Didham RK, Hammond PM, Lawton JH, Eggleton P, Stork NE (1998) Beetle species responses to tropical forest fragmentation. Ecological Monographs, 68, 295-323.

Dodds WK, Gido K, Whiles MR, Fritz KM, Matthews WJ (2004) Life on the edge: The ecology of Great Plains prairie streams. Bioscience, **54**, 205-216.

Driver LJ, Adams GL (2013) Life history and spawning behavior of the Western Sand Darter

(*Ammocrypta clara*) in Northeast Arkansas. American Midland Naturalist, **170**, 199-212.

Dudgeon D, Arthington AH, Gessner MO *et al.* (2006) Freshwater biodiversity: Importance threats, status and conservation challenges. Biological Reviews*,* **81**, 163-182.

Erös T (2007) Partitioning the diversity of riverine fish: The roles of habitat types and non-native species. Freshwater Biology, **52**, 1400-1415.

Estes JA, Palmisano JF (1974) Sea otters: Their role in structuring nearshore communities. Science, **185**, 1058–1060.

Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. Ecological Monographs, **65**, 75-100.

Evans, HC, Elliot SL, Hughs DP (2011) Ophiocordyceps unilateralis: A keystone species for unraveling ecosystem functioning and biodiversity of fungi in tropical forests? Communicative and Integrative Biology,**4**, 598-602.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics, **34**, 487-515.

Fencl JS, Mather ME, Costigan KH, Daniels MD (2015) How big of an effect do small dams have? Using geomorphological footprints to quantify spatial impact of low-head dams and identify patterns of across-dam variation. PLOS One, **10**, e0141210. doi:10.1371/journal.pone.0141210.

Fischer JR, Quist MC (2014) Characterizing lentic freshwater fish assemblages using multiple sampling methods. Environmental Monitoring and Assessment, **186**, 4461-4474.

Floury M, Usseglio-Polatera P, Ferreol M, Delattre C, Souchon Y (2013) Global climate change in large European rivers: Long-term effects on macroinvertebrate communities and potential local confounding factors. Global Change Biology, **12**, 1085-1099.

Forman RTT, Godron M (1986) Landscape ecology. John Wiley and Sons, New York.

Frissell CA, Liss WJ, Warren CE, Hurley MD (1986) A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. Environmental Management, **10**, 199-214.

Gilbert LE (1980) Food web organization and conservation of Neotropical biodiversity. In: Conservation Biology (eds Soulé ME, Wilcox BA), pp. 11–33, Sinauer, Sunderland, Massachusetts, USA.

Greig S, Sear D, Carling P (2007) A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. Hydrological processes, **21**, 323-334.

Hagen CA, Grisham BA, Boal CW, Haukos DA (2013) A meta-analysis of lesser prairie-chicken nesting and brood-rearing habitats: Implications for habitat management. Wildlife Society Bulletin, **37**, 750-758.

Hakala JP, Hartman KJ (2004) Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. Hydrobiologia, 515, 203-213.

Harrison AB, Slack WT, Killgore KJ (2014) Feeding habitats of young-of-year river sturgeon *Scaphirhyncus* spp. In the Lower Mississippi River. American Midland Naturalist, 171, 54-67.

Harvey GL, Clifford NJ (2009) Microscale hydrodynamics and coherent flow structures in rivers: Implications for the characterization of physical habitat. River Research and Applications, **25**, 160-180.

Hauer C, Unfer G, Tritthart M, Formann E, Habersack H (2011) Variability of mesohabitat characteristics in riffle-pool reaches: Testing an integrative evaluation concept (FGC) for MEM-application. River Research and Applications, **27**, 403-430.

Hauer C, Unfer G, Holzmann H, Schmutz S, Habersack H (2013) The impact of discharge change on physical instream habitats and its response to river morphology. Climatic Change, **116**, 827-850.

Hawkins CP, Kershner JL, Bisson PA (1993) A hierarchical approach to classifying stream habitat features. Fisheries, **18**, 3–12.

Heino J, Muotka T, Paavola R, Hamalainen H, Koskenniemi E (2002) Correspondence between regional delineations and spatial patterns in macroinvertebrate assemblages of boreal headwater streams. Journal of the North American Benthological Society, **21**, 397-413.

Herzog DP, Ostendorf DE, Hrabik RA, Barko VA (2009) The mini-Missouri trawl: A useful methodology for sampling small-bodied fishes in small and large river systems. Journal of Freshwater Ecology, **24**, 103-108.

Hessen DO, Kaartdvedt S (2014) Top-down cascades in lakes and oceans: different perspectives but same story? Journal of Plankton research, **36**, 914-924.

Hintz WD, Porreca AP, Garvey JE, Phelps QE, Tripp SJ, Hrabik RA, Herzog DP (2015) Abiotic attributes surrounding alluvial islands generate critical fish habitat. River Research and Applications, **31**, 1218-1226.

Hintz WD, Glover DC, Garvey JE (2016) Status and Habitat Use of *Scaphirhynchus* Sturgeons in an Important Fluvial Corridor: Implications for River Habitat Enhancement. Transaction of the American Fisheries Society, 145, 386-399.

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology, 12, 197-229.

Hooper DU, Chapin III FS, Ewel JJ *et al.* (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs, **75**, 3-35.

Hurlbert SH (1997) Functional importance *vs.* keystoneness: Reformulating some questions in theoretical biocenology. Australian Journal of Ecology, **22**, 369–382.

Hynes H (1970) The ecology of running waters. University of Toronto Press, Toronto.

IPCC (2013) Summary for policymakers. In: Climate change 2013: the physical science basis. (eds Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Isaak DJ, Thurow RF, Rieman BE, Dunham JB (2007) Chinook salmon use of spawning patches: Relative roles of habitat quality, size, and connectivity. Ecological Applications, **17**, 352-364.

Jaeger KL, Olden JD, Pelland NA (2014) Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. Proceedings of the National Academy of Sciences of the United States of America, **111**, 13894-13899.

 Jelks HL, Walsh SJ, Burkhead NM *et al.* (2008) Conservation Status of imperiled North American fishes. Fisheries, **33**, 372-407.

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos, **69**, 373–386.

Juracek KE, Perry CA (2005) Gravel sources for the Neosho River in Kansas, 2004. United States Geological Survey Scientific Investigations Report 2005–5282.

Kenner MC, Estes JA, Tinker MT *et al.* (2013) A multi-decade time series of kelp forest community structure at San Nicolas Island, California (USA). Ecology, **94,** 2654.

Kiernan JD, Moyle PB, Crain PK (2012) Restoring native fish assemblages to a regulated

California stream using the natural flow regime concept. Ecological Applications, **22**, 1472-1482.

Kirk JP, Slack WT, George SG, Killgore KJ (2010) A preliminary evaluation of trawling for young-of-year Gulf sturgeon. Proceedings of the Annual Conference Southeast Association of Fish and Wildlife Agency, **64**, 168–171.

Kleindl WJ, Rains MC, Marshall LA, Hauer FR (2015) Fire and flood expand the floodplain shifting habitat mosaic concept. Freshwater Science, **34**, 1366-1382.

Kotliar NB (2000) Application of the new keystone-species concept to prairie dogs: How well does it work? Conservation Biology, **14**, 1715-1721.

Kruess A (2003) Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. Ecography, **26**, 283–290.

Kwik JTB, Yeo DCJ (2015) Differences in fish assemblages in protected and non-protected freshwater streams in a tropical urbanized country. Hydrobiologia, **762**, 143-156.

Lake PS (2003) Ecological effects of perturbation by drought in flowing waters. Freshwater Biology, **48**, 1161-1173.

Lautz LK, Fanelli RM (2008) Seasonal biogeochemical hotspots in the streambed around restoration structures. Biogeochemistry, **91**, 85-104.

Law BS, Dickman CR (1998) The use of habitat mosaic by terrestrial vertebrate fauna: Implications for conservation and management. Biodiversity and Conservation, 7, 323-333.

Legendre P, Legendre L (1998) Numerical ecology. 2nd edition. Elsevier, Amsterdam.

Li H, Reynolds JF (1995) On definition and quantification of heterogeneity. Oikos, **73**, 280–284.

Lowe WH, Likens GE, Power ME (2006) Linking scales in stream ecology. Bioscience, **56**, 591-597.

Machtans CS, Villard MA, Hannon SJ (1996) Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology, **10**, 1366-1379.

Maes J, Paracchini ML, Zulian G, Dunbar MB, Alkamade R (2012) Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. Biological Conservation, **155**, 1-12.

Magle SB, Angeloni LM (2011) Effects of urbanization on the behaviour of a keystone species. Behaviour, **148**, 31–54.

Magoulick DD, Kobza RM (2003) The role of refugia for fishes during drought: a review and synthesis. Freshwater Biology, **48**, 1186-1198.

Malard F, Tockner K, Dole-Olivier MJ, Ward JV (2002) A landscape perspective of surface-subsurface hydrological exchanges in river corridors. Freshwater Biology, **47**, 621-640.

Manly BFJ (1986) Multivariate statistical methods: A primer. Chapman and Hall Press, London.

Matono P, Bernardo JM, Costa AM, Ilhéu M (2014) Fish Response to Anthropogenic Pressures in Temporary Streams: The Importance of Environmental Drivers. River Research and Applications, **30**, 1281-1295.

Matthews WJ, Harvey BC, Power ME (1994) Spatial and temporal patterns in the fish assemblages of individual pools in a Midwestern stream (USA). Environmental Biology of Fishes, **39**, 381-397.

McCain M, Fuller D, Decker L, Overton K (1990) Stream habitat classification and inventory procedures for northern California. FHC Currents. No.1. U.S. Department of Agriculture. Forest Service, Pacific Southwest Region.

McClain ME, Boyer EW, Dent CL *et al.* (2003) Biogeochemical hotspots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems, **6**, 301-312.

McGarigal K, Cushman S, Ene E (2012) FRAGSTATS V4: Spatial pattern analysis program for categorical and continuous maps, computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html

Meehl GA, Arblaster JM, Tebaldi C (2005) Understanding future patterns of increased precipitation intensity in climate model simulations. Geophysical Research Letters, **32**, L18719.

Menge BA, Berlow EL., Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept: Variation in interaction strength in a rocky intertidal habitat. Ecological Monographs, **64**, 249–286.

Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio, **69**, 89-107.

Mishra V, Cherkauer KA, Shukla S (2010) Assessment of Drought due to Historic Climate Variability and Projected Future Climate Change in the Midwestern United States. Journal of Hydrometeorology, **11**, 46-68.

Mouquet N, Gravel D, Massol F, Calcagno V (2013) Extending the concept of keystone species to communities and ecosystems. Ecology Letters, **16**, 1-8.

Mills LS, Soulé ME, Doak DF (1993) The keystone species concept in ecology and conservation. BioScience, **43**, 219–224.

Naiman RJ, Melillo JM, Hobbie JE (1986) Alteration of North American streams by beaver (*Castor canadensis*). Ecology, **67**, 1254–1289.

Naskar M, Sahu SK, Sharma AP (2015) Assessment of fish species assemblage on mesohabitat scale: A case of middle stretch of Narmada River, India. Aquatic Ecosystem Health & Management, **18**, 232-239.

Newson MD, Newson CL (2000) Geomorphology, ecology and river channel habitat: Mesoscale approaches to basin-scale challenges. Progress in Physical Geography, **24**, 195–217.

Oksanen J, Blanchet FG, Kindt R *et al.* (2013) Vegan: Community ecology package. R package version 2.0-9. http://CRAN.R-project.org/package=vegan.

Paine RT (1966) Food web complexity and species diversity. The American Naturalist, **100**, 65–75.

Paine RT (1969) A note on trophic complexity and community stability. American Naturalist, **103**, 91-93.

Pall P, Aina T, Stone DA *et al.* (2011) Anthropogenic greenhouse gas contribution to flood risk in England and Wales in autumn 2000. Nature, **470**, 382-385.

Parr TB, Cronan CS, Danielson TJ, Tsomides L, Simon KS (2016) Aligning indicators of community composition and biogeochemical function in stream monitoring and ecological assessments. Ecological Indicators, **60**, 970-979.

Pichon CL, Tales É, Gorges G, Baudry J, Boët P (2015) Using a continuous riverscape survey to examine the effects of the spatial structure of functional habitats on fish distribution. Journal of Freshwater Ecology, **31**, 1-19.

Power ME, Mathews WJ, Stewart AJ (1985) Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. Ecology, **66**, 1448-1456.

Power ME, Tilman D, Estes JA *et al.* (1996) Challenges in the quest for keystones. Bioscience, **46**, 609-620.

Pratt TC, Gardner WM, Watkinson DA, Bouvier LD (2016) Ecology of the River Darter in Canadian waters: Distribution, relative abundance, life-history traits, diet, and habitat characteristics. Diversity, **8**, 1-16.

Pringle CM, Naiman RJ, Bretschko G *et al.* (1988) Patch dynamics in lotic systems: The stream as a mosaic. Journal of the North American Benthological Society, **7**, 503-524.

R Core Development Team (2013) R: A language and environment for statistical computing. R foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/.

Roche B, Benbow ME, Merritt R *et al.* (2013) Identifying the Achilles heel of multi-host pathogens: The keystone 'host' species illustrated by Mycobacterium ulcerans transmission. Environmental Research Letters, **8**, 1-7.

Rosenberger A, Angermeier PL (2003) Ontogenic shifts in habitat use by the endangered Roanoke logperch (*Percina rex*). Freshwater Biology, **48**, 1563-1577.

Schindler DE, Hodgson JR, Kitchell JF (1997) Density-dependent changes in individual foraging specialization of largemouth bass. Oecologia, 110, 592-600.

Schlosser IJ (1982) Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs, **52**, 395-414.

Schlosser IL (1987) A conceptual framework for fish communities in small warmwater streams. In: Community and evolutionary ecology of North American stream fishes (eds Matthews WJ, Heins DC), pp. 17-24, University of Oklahoma Press, Norman, Oklahoma.

Schwartz JS, Herricks EE (2008) Fish use of ecohydraulic-based mesohabitat units in a low-gradient Illinois stream: implications for stream restoration. Aquatic Conservation: Marine and Freshwater Ecosystems, **18**, 852.

Schwartz JS, Neff KJ, Dworak FE, Woockman RR (2015) Restoring riffle-pool structure in an

incised, straightened urban stream channel using an ecohydraulic modeling approach. *Ecological Engineering*, **78**, 112-126.

Silva DRO, Ligeiro R, Hughes RM, Callisto M (2014) Visually determined stream mesohabitats influence benthic macroinvertebrate assessments in headwater streams. Environmental Monitoring and Assessment, **186**, 5479-5488.

Small GE, Pringle CM, Pyron M, Duff JH (2011) Role of the fish *Astyanax aeneus* (Characidae) as a keystone nutrient recycler in low-nutrient Neotropical streams. Ecology, 92, 386-397.

Smith JM, Mather ME (2013) Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. Freshwater Biology*, **58**, 1523-1538.

Stanley EH, Fisher SG, Grimm NB (1997) Ecosystem expansion and contraction in streams. Bioscience*, **47**, 427-435.

Starks TA, Long JM, Dzialowski AR (2015) Community structure of age-0 fishes in paired mainstem and created shallow-water habitats in the Lower Missouri River. River Research and Applications, **32**, 753-762.

Stefanescu C, Herrando S, Pàramo F (2004) Butterfly species richness in the north-west Mediterranean Basin: The role of natural and human-induced factors. Journal of Biogeography, **31**, 905-915.

Strahler AN (1957) Quantitative analysis of watershed geomorphology. Transactions American Geophysical Union, **38**, 913-920.

Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology, **73**, 747-754.

Stouffer DB, Sales-Pardo M, Sirer MI, Bascompte J (2012) Evolutionary conservation of species' roles in food webs. Science, **335**, 1489–1492.

Taylor CM (2000) A large-scale comparative analysis of riffle and pool fish communities in an upland stream system. Environmental Biology of Fishes, **58**, 89-95.

Teichert N, Valade P, Bosc P, Richarson M, Gaudin P (2013) Spawning-habitat selection of an Indo-Pacific amphidromous gobiid fish, *Sicyopterus lagocephalus* (Pallas). Marine and Freshwater Research, **64**, 1058-1067.

Tews J, Brose U, Grimm V, Tielbörger V, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. Journal of Biogeography, **31**, 79–92.

Tiemann JS, Gillette DP, Wildhaber ML, Edds DR (2004) Effects of lowhead dams on riffle-dwelling fishes and macroinvertebrates in a Midwestern river. Transactions of the American Fisheries Society, **133**, 705-717.

Turner MG, Gardner RH, O'Neill RV (2001) Landscape ecology in theory and practice. Springer-Verlag, New York.

Utne-Palm AC, Salvanes AGV, Currie B (2010) Trophic structure and community stability in an overfished ecosystem. Science, **329**, 333-336.

Vaughn CC (2010) Biodiversity losses and ecosystem function in freshwaters: Emerging conclusions and research directions. Bioscience, 60, 25-35.

Venables WN, Ripley BD (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Villemey A, van Halder I, Ouin A *et al.* (2015) Mosaics of grasslands and woodlands is more effective than habitat connectivity to conserve butterflies in French farmland. Biological

Conservation, **191**, 206-215.

Vörösmarty CJ, Mcintyre PB, Gessner MO *et al.* (2010) Global threats to human water security
and river biodiversity. Nature*,* **467**, 555-561.

Wentworth CK. (1922) A scale of grade and class terms for clastic sediments. Journal of
Geology, **30**, 377–392.

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon, **21**, 213-251.

Williams NM, Kremen C (2007) Resource distributions among habitats determine solitary bee
offspring production in a mosaic landscape. Ecological Applications, **17**, 910-921.

Wilson MC, Chen XY, Corlett RT *et al.* (2016) Habitat fragmentation and biodiversity
conservation: Key findings and future challenges. Landscape Ecology, **31**, 219-227.

Winemiller KO, Flecker AS, Hoeinghaus DJ (2010) Patch dynamics and environmental
heterogeneity in lotic ecosystems. Journal of the North American Benthological Society*,*
29, 84-99.

Figure 1.1. Conceptual figure of research including overarching question, specific research questions, predictions, goals, and implications. Determining physical differences of mesohabitats (Q1) is a precursor to mapping site-specific mosaics (Q2). For these isolated and connected physical habitat templates, we measured isolated mesohabitat (Q3) and connected mosaic (Q4) biodiversity. To advance future research, we ask if the extensive literature on keystone species can guide future keystone habitat research (Q5). As a result of our research, conservation planning for impacted habitats can be more effective.

Overarching Question: Do specific types of habitats have disproportionate effects on biodiversity?

Q1. Are the types of habitat patches discrete?

Pool
Riffle
Run

Determine habitat-specific physical differences

Q2. Does the combination of co-occurring habitat patches vary across sites?

Quantify mosaic patch composition

Q3: Does biodiversity differ among mesohabitats?

Relate biota to individual habitats

Q4. Do keystone habitats exist?

Stream habitat mosaic

Keystone habitat

* Keystone habitat in mosaic

Relate biota to connected mosaics of habitats

Q5: Can the predictions from the keystone species literature inform the keystone habitat concept?

Top predator
Secondary consumer
Primary consumer
Primary producer

Run   Pool   Riffle
?

Compare underlying organization of keystones

Implications: Identifying keystones can improve habitat planning & conservation outcomes in face of global change.

Figure 1.2. Map of study area including (a) Neosho River within the state of Kansas, and (b) ten 3-km sampling sites within the Upper Neosho River sub-drainage along the Neosho and Cottonwood Rivers, KS below five low-head dam sites (black dots) and at five undammed sites (gray dots). Note: habitat below dammed and undammed sites was not statistically different.
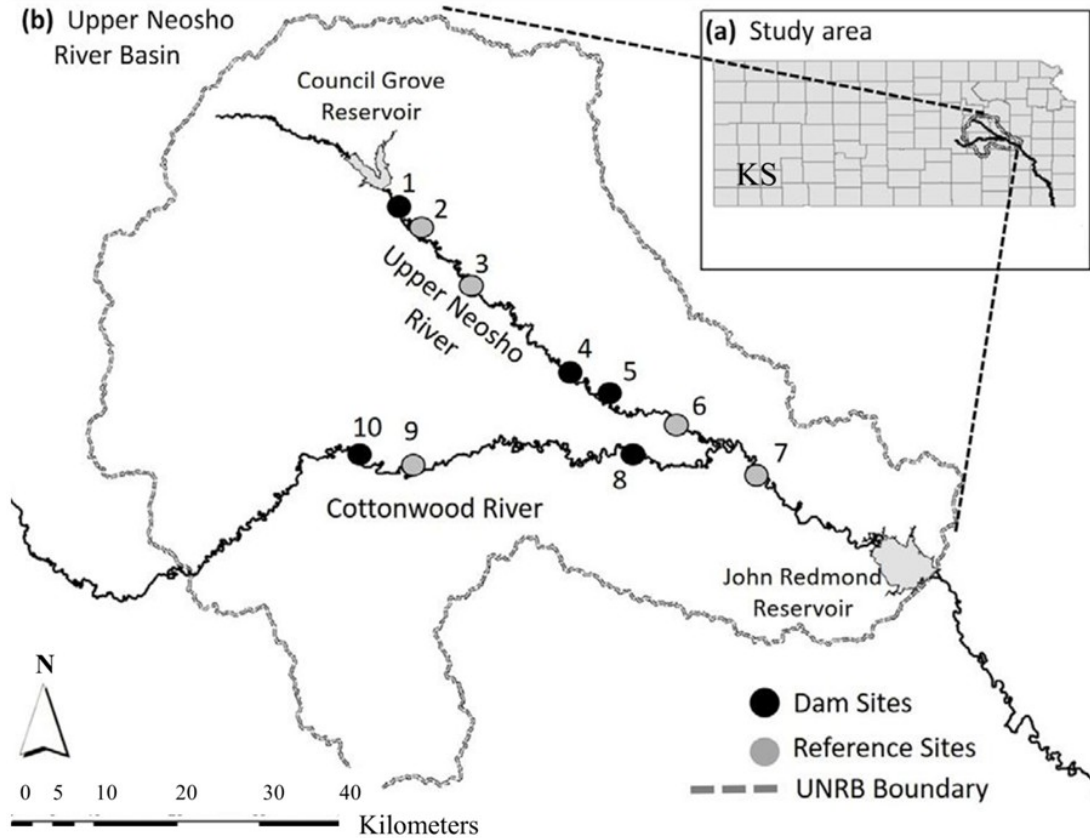
Figure 1.3. An evaluation of three environmental variables (water depth, flow velocity, substrate size) is shown to quantitatively assess if mesohabitats were discrete. A biplot (a) of the first two axes of the linear discriminant function analysis shows the discriminant function statistic (Wilk's lambda), which was used to show the separation among mesohabitat types. Three-dimensional scatterplots (b) of environmental variables (x-axis velocity, y-axis substrate, z-axis depth) for each mesohabitat category. Pool, riffle, run, and glide mesohabitats are indicated in blue, green, red, and purple.
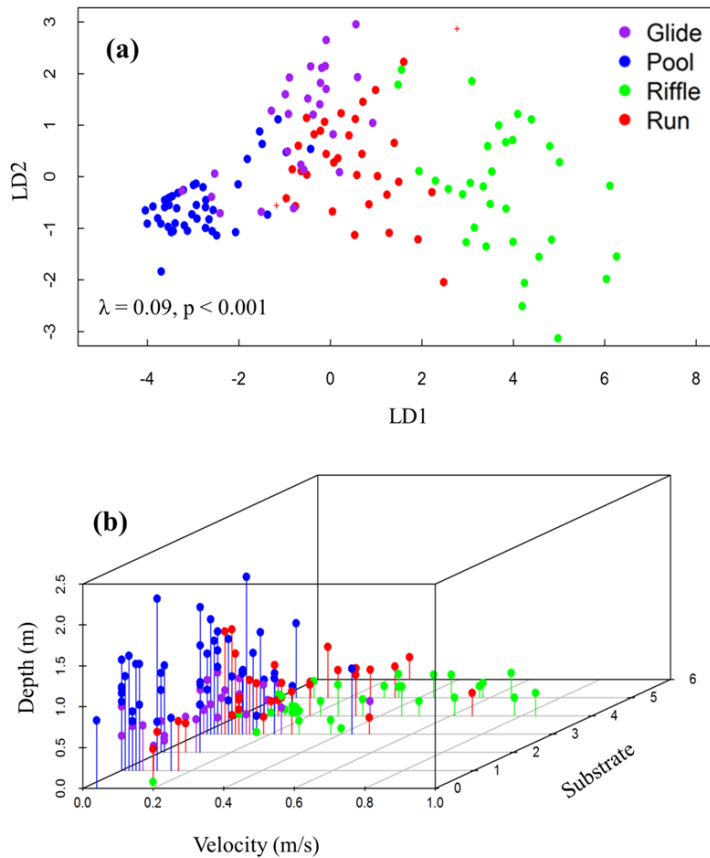
Figure 1.4. Maps illustrating habitat mosaics (composed of variable patterns of pool, riffle, run, and glide mesohabitats indicated in blue, green, red, and purple patches) at ten sample sites within our Upper Neosho River sub-drainage study location. Sites include (a) #1-Riverwalk, (b) #2-Reference 1, (c) #3-Reference 2, (d) #4-Ruggles, (e) #5-Emporia, (f) #6-Reference 3, (g) #7-Reference 4, (h) #8-Soden, (i) #9-Reference 5, (j) #10-Cottonwood Falls. Maps were oriented to fit within figure. The white arrow indicates true north.
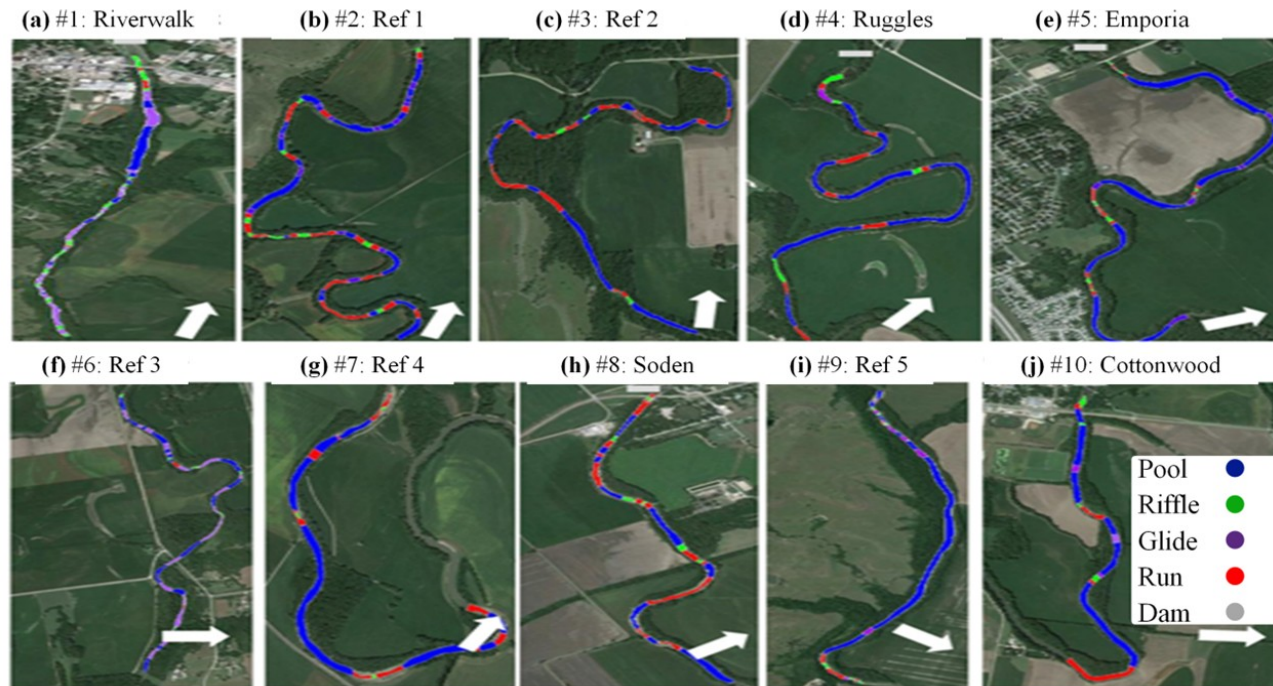
Figure 1.5. Non-metric multidimensional scaling biplots for (a) abundance for entire fish community (stress = 0.197; ANOSIM Global R = 0.24, p < 0.001) and (b) presence-absence for entire fish community (stress = 0.259; ANOSIM Global R = 0.20, p < 0.001) at ten sample sites located along the Neosho and Cottonwood Rivers, KS. Ellipses indicate 95% confidence intervals. Pool, riffle, run, and glide mesohabitats are indicated in blue, green, red, and purple.
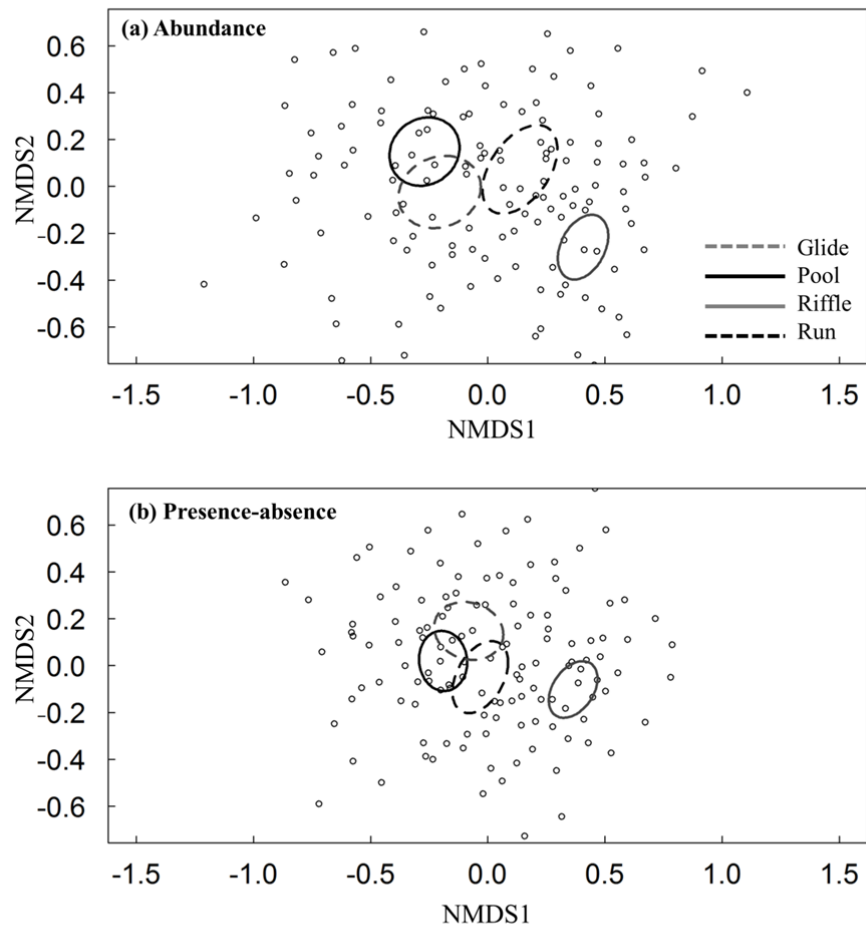
Figure 1.6. (a) Stacked bar plot of the relative proportion of mesohabitats (pool, riffle, run, glide) at each of ten sample sites along the Neosho and Cottonwood Rivers, KS. (b) Mean patch size (ha) for each mesohabitat type. Pool, riffle, run, and glide mesohabitats are indicated in blue, green, red, and purple.
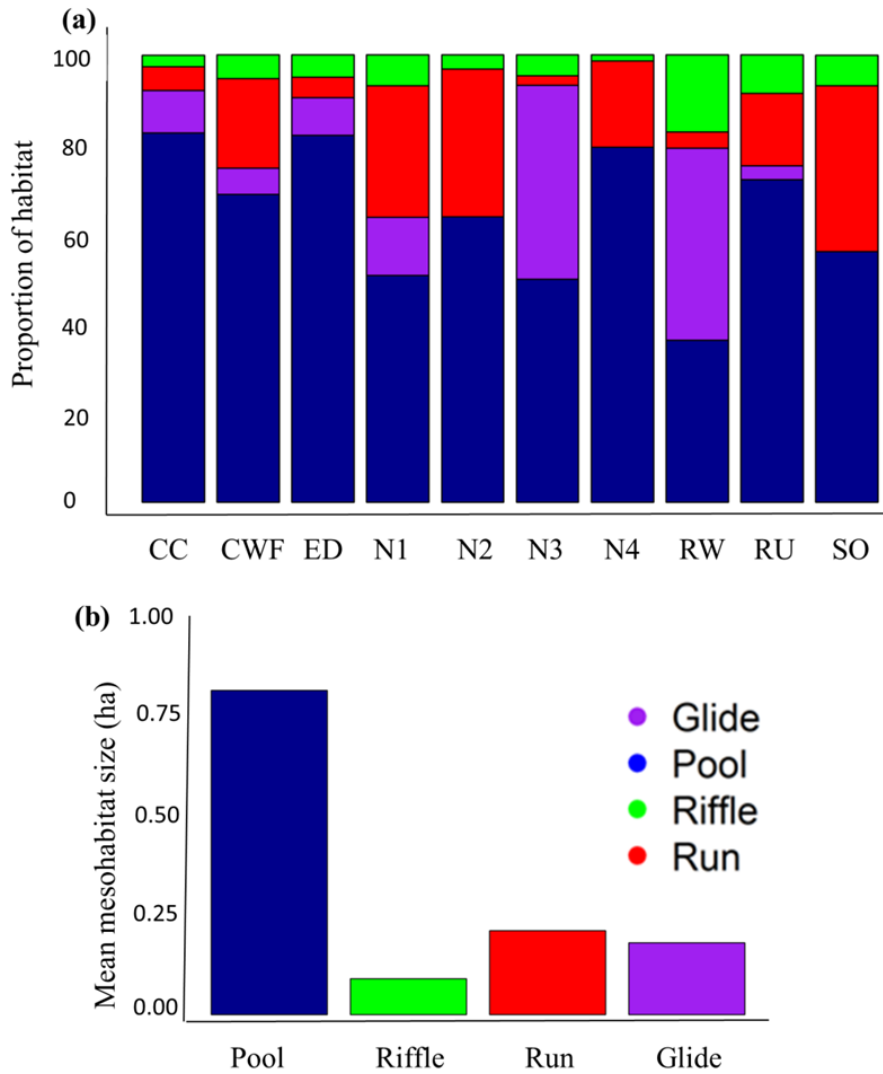
Figure 1.7. (a) Mean species richness (# of individual species / 30 m transect) across mesohabitats and species richness weighted by the proportion of each mesohabitat. Errors bars represent 2 SE. Asterisks denote statistical significance (α = 0.05; Kruskal-Wallis test and multiple comparisons).
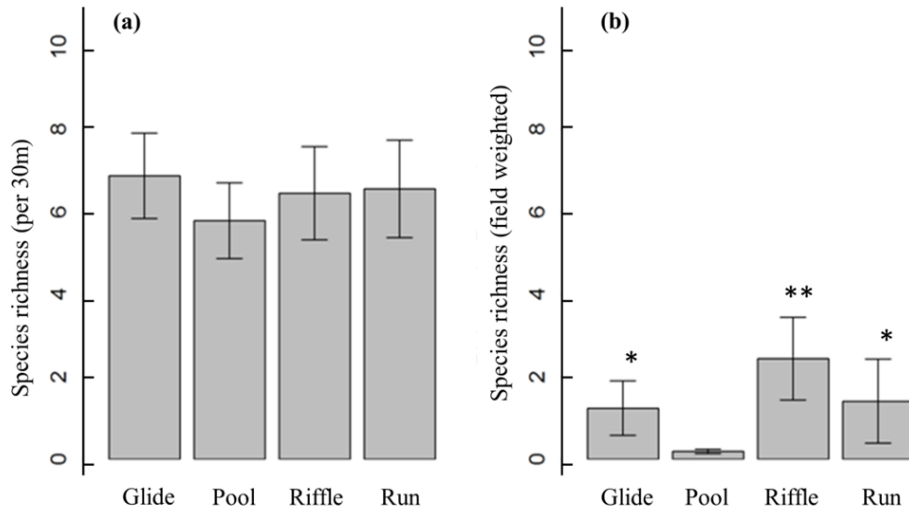
Figure 1.8. Regression plots of species richness (Y) and (a) habitat diversity (Shannon's H'), (b) riffle density, (c) pool density, (d) run density and (e) glide density at ten sample sites along the Neosho and Cottonwood Rivers, KS. Trend lines were added where regression analysis revealed significant relationships ($\alpha = 0.05$).
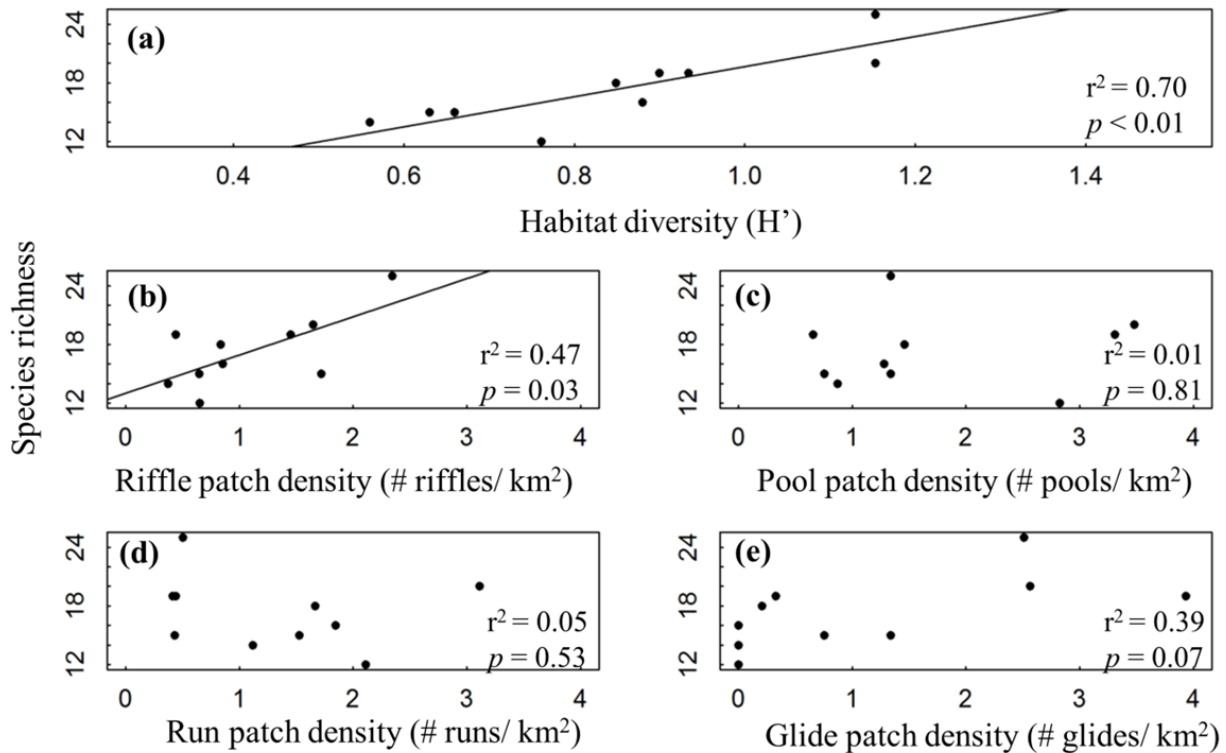
Figure 1.9. Multimodel inference results shows that riffles are keystone habitats and have the largest influence (i.e., slope) on habitat diversity (Y) and species richness (Y) in the context of all mesohabitats (X1-X4) in multiple regressions. Shown are model-averaged slopes for the responses (a) habitat diversity, measured as Shannon's H', and (b) species richness.
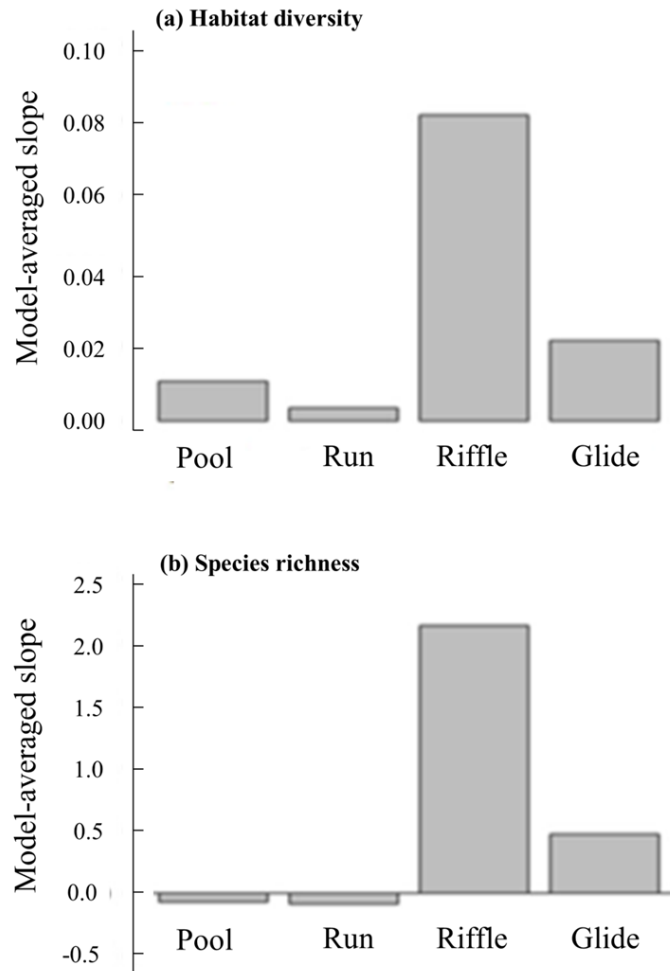
Chapter 2 - Habitat mosaics and path analysis can improve biological conservation of aquatic biodiversity in ecosystems with low-head dams

Abstract

Conserving native biodiversity depends on restoring functional habitats in the face of human-induced disturbances. Low-head dams are a ubiquitous human impact that degrades aquatic ecosystems worldwide. To improve our understanding of how low-head dams impact habitat and associated biodiversity, our research examined complex interactions among three spheres of the total environment. i.e., how low-head dams (*anthroposphere*) affect aquatic habitat (*hydrosphere*), and native biodiversity (*biosphere*) in streams and rivers. Creation of lake-like habitats upstream of low-head dams is a well-documented major impact of dams. Alterations downstream of low head dams also have important consequences, but these downstream dam effects are more challenging to detect. In a multidisciplinary field study at five dammed and five undammed sites within the Neosho River basin, KS, we tested hypotheses about two types of habitat sampling (transect and mosaic) and two types of statistical analyses (analysis of covariance and path analysis). We used fish as our example of biodiversity alteration. Our research provided three insights that can aid environmental professionals who seek to conserve and restore fish biodiversity in aquatic ecosystems threatened by human modifications. First, a mosaic approach identified habitat alterations below low-head dams (e.g. increased proportion of riffles) that were not detected using the more commonly-used transect sampling approach. Second, the habitat mosaic approach illustrated how low-head dams reduced natural variation in stream habitat. Third, path analysis, a statistical approach that tests indirect effects, showed how

dams, habitat, and fish biodiversity interact. Specifically, path analysis revealed that low-head dams increased the proportion of riffle habitat below dams, and, as a result, indirectly increased fish species richness. Furthermore, the pool habitat that was created above low-head dams dramatically decreased fish species richness. As we show here, mosaic habitat sampling and path analysis can help conservation practitioners improve science-based management plans for disturbed aquatic systems worldwide.

Introduction

Managing the adverse impacts of low-head dams on aquatic biodiversity is an urgent but complex biological conservation challenge that requires combining insights from the hydrosphere, biosphere, and anthroposphere (Cooper et al., 2017). Low-head dams (< 4 m in height) are ubiquitous worldwide with as many as 2 million of these small barriers fragmenting river ecosystems in the U.S. alone (Graf, 1993; Poff et al., 1997). In spite of the widespread distribution of these disturbances, the ecological effects of low-head dams on riverine ecosystems remain poorly understood (Benstead et al., 1999; Poff and Hart, 2002; Fencl et al., 2015). Creation of upstream, lake-like reservoir habitats and the consequent reduction of native biodiversity are well-documented hydrological and biological impacts of low-head dams (Ward and Stanford, 1979; Watters, 1996; Santucci et al., 2005; Fencl et al., 2017). However, changes in habitat and biota downstream of low-head dams can also have important impacts on natural communities and ecosystems. These downstream dam effects are often more challenging to detect (e.g., Fencl et al., 2017). Here we evaluate how man-made low-head dams impact habitat and associated native biodiversity (Fig. 2.1) by comparing two approaches to quantifying habitat (mosaic and transect) and two statistical analyses [analysis of covariance (ANCOVA) and path

analysis]. Additional tools for detecting low-head dam impacts on habitat and biodiversity will help conservation efforts of state and federal environmental agencies that seek to monitor, manage, repair, or prioritize the removal of low-head dams (Bellmore et al., 2016; Tullos et al., 2016).

Environmental professionals increasingly seek to understand and manage the effects of low-head dams (Gillette et al., 2005; Santucci et al., 2005; Slawski et al., 2008). Low-head dams have been shown to directly impact lotic ecosystems by fragmenting stream corridors (Dodd et al., 2003; Chick et al., 2006), altering the natural flow regime (Poff et al., 1997; Csiki and Rhoads, 2010; Yan et al., 2013) or blocking the dispersal of aquatic organisms (Benstead et al., 1999; Helfrich et al., 1999; Rahel, 2007). As climate change continues to degrade lotic systems (Beatty et al., 2017), dam repair and removal will be implemented globally to restore connectivity and improve fluvial health (Tonra et al., 2015). Since most dams are relatively small structures (Bellmore et al., 2016), evaluation of low-head dam impacts, as we provide here, is critical to the success of dam repair and removal efforts (Poff and Hart, 2002). A focus on habitat and landscape metrics to understand dam effects on biodiversity is essential for effective watershed management (Cheng et al., 2016).

A transect approach assesses habitat conditions at regular intervals (e.g., transects or other repeated data collection units) over a spatially extensive area (Platts et al., 1983; Fitzpatrick et al., 1998; Hauer and Lamberti, 2007). This commonly used approach to habitat sampling measures point-specific environmental characteristics (e.g., width, depth, velocity, and substrate) at systematically-placed sampling points along the stream channel (Simonson et al., 1994; Fitzpatrick et al., 1998). For example, transects can be spaced two-three times the mean stream width (Krause et al., 2013) for an extent of 13-20 transects (Simonson et al., 1994) or up to 35

stream widths (Lyons, 1992). Transects have also been used within specific habitat units (Tiemann et al., 2004; Weaver et al., 2014), typically for habitats > 50% of the channel width (e.g. Fitzpatrick et al., 1998). An advantage of the habitat transect approach is that this frequently-used method maximizes repeatability and precision of measurements at regular, representative intervals over a large spatial scale while minimizing subjective bias (Platts et al., 1983; Simonson et al., 1994; Fitzpatrick et al., 1998). Disadvantages of the transect approach are that this method emphasizes the dominant habitat, may fail to detect underlying heterogeneity created by less common habitat patches, and can miss connections and interactions among habitat patches that may be important for biodiversity.

The mosaic approach provides an alternative method for quantifying habitat. Lotic ecosystems can be viewed as mosaics (defined as interconnected habitat patches) that individually vary in structure and function and together create complex but predictable patterns of heterogeneity (Hitchman Chapter 1). Consequently, the mosaic approach quantifies type and arrangement of aquatic mesohabitat patches (e.g., pool, riffle, run, and glide; Jowett, 1993) that individually have been linked to aquatic community structure (Yeiser and Richter, 2015; Cheek et al., 2016). An advantage of the mosaic approach is that this method considers compositional and configurational metrics that can detect underlying ecological patterns for both common and uncommon habitat patches. Because the spatial configuration and composition of patches affect biological patterns and processes (Pringle et al., 1988; Lowe et al., 2006; Pichon et al., 2016), viewing streams as a connected habitat mosaic may improve the chances of detecting downstream impacts of anthropogenic disturbances, such as low-head dams, on both the hydrosphere and biosphere.

Choice of statistical approach can affect the ability of environmental professionals to detect low-head dam impacts on habitat and biodiversity. Most common statistical approaches assume direct effects between independent and dependent variables (e.g. general and generalized linear models including analysis of variance, ANCOVA, multiple regression; Dodd et al., 2003; Greathouse et al., 2006) or identify direct patterns related to multiple variables (e.g. ordination analyses including non-metric multidimensional scaling, canonical correspondence analysis; Helms et al., 2011, Chu et al., 2015; Hastings et al., 2016). Less often used are statistical techniques that quantify both direct and indirect effects including how independent variables affect a response variable as mediated through a third set of variables (e.g., path analysis). When used, path analysis has provided new information about how stream flow metrics (Bruder et al., 2017), land-use (Taka et al., 2016), and beaver dams (Smith and Mather, 2013) affect aquatic communities and ecosystems. Most researchers do not set out to look for mediated statistical effects when studying dam impacts on biodiversity and habitat alteration, but this less frequently-used approach to statistical analysis may provide new ecological understanding about subtle but important downstream effects of low-head dams.

Here we tested four research hypotheses (Fig. 2.1) using fish species richness as a proxy for biodiversity. First, do transect and mosaic approaches provide different research and conservation insights about habitat patterns below low-head dams compared to undammed sites (Q1)? We predicted that mosaics of common and rare habitats will better distinguish dammed from undammed sites because of increased resolution. Second, as an extension of the previous question, do dammed and undammed sites differ in habitat variability (Q2)? Because many human impacts simplify the environment, we predicted that dams could reduce natural habitat variability. Third, using a frequently-used general linear model, ANCOVA, do transect and

mosaic habitat approaches show different dam-habitat-fish biodiversity patterns downstream of dams and at undammed sites (Q3)? As noted above, we predicted that the additional resolution provided by habitat mosaics would better discriminate fish biodiversity patterns at dammed and undammed sites. Fourth, for both transect and mosaic habitat data, does a less-common statistical approach that can detect mediated effects (e.g., path analysis) provide new knowledge about dam-habitat-fish relationships both downstream (Q4a; dammed vs. undammed site comparisons) and upstream of dams (Q4b; upstream vs. downstream of low-head dam)? In this research, our focus was primarily on impacts downstream of dams. However, because habitat alteration is a conservation concern both upstream and downstream of dams, we also included the upstream-downstream comparison as a way to ground truth the path analysis approach on a well-documented dam impact (Q4b). In addition, combining upstream and downstream alterations allowed us to assess the basin-wide implications of these co-occurring dam-effects.

Materials and Methods

Study Area

Our study was conducted along the upper Neosho River and lower Cottonwood River, two 5th order streams located within the Upper Neosho River basin (UNRB), KS, USA. The UNRB drains approximately 7,770 km2 upstream of the John Redmond Reservoir in Morris, Lyon, and Chase Counties, KS. Flow within the UNRB is influenced by six intact low-head dams which impound approximately 14,000 km2 of water (Fencl et al., 2015). The Upper Neosho and Cottonwood Rivers lie predominately on Permian age limestone and shale bedrock overlain by Quaternary alluvium (Juracek and Perry, 2005). Land use is dominated by row-crop agricultural fields and characterized by small riparian zones (Tiemann et al., 2004). Baseflow

conditions (5.0-32.0 m3/s, Neosho River, USGS gage 07179730; 13.0-19.0 m3/s Cottonwood

River, USGS gage 07182250) were similar at the time of sampling.

General Sampling Regime

Sampling occurred during baseflow conditions at five low-head dam sites and at five

undammed sites (Fig. 2.2). With this design, we sampled all intact low-head dams in the UNRB

except for Correll Dam (between sites 3 and 4) to which we were denied access by the

landowner. Our sites were constrained by large, Army Corp of Engineers dams at Council Grove

and Marion Reservoirs at the upper boundaries of the Neosho and Cottonwood Rivers,

respectively and by the John Redmond Reservoir at the lower boundary of the study area. For

this purpose, we distinctly use the term "undammed" to refer to sites that are not in close

proximity to low-head dams (> 5km) instead of terms suggesting natural or control locations.

The term "dammed" referred to low-head dam sites. Dammed (1, 4, 5, 8, 10) sites were

interspersed with undammed sites (2, 3, 6, 7, 9) and separated by at least 5 km. Because

geomorphological footprints of the low-head dams within the study area are less than 2 km

(Fencl et al., 2015), this separation of > 5 km between dammed sites and undammed ensured that

the undammed sites were outside of the immediate dam impact zone while still close enough to

share similarity in geomorphology and other site-specific characteristics. Six sites (1-6) were

located along the Upper Neosho River (Fig. 2.2). Site 7 was located just below the confluence of

the Neosho and Cottonwood Rivers (Fig. 2.2). Three sites (8-10) were located on the

Cottonwood River (Fig. 2.2). A Chi-square test found no significant differences in mesohabitat

between the Neosho and Cottonwood Rivers ($\chi^2 = 2.42$; p = 0.49, Fig. 2.3).

Specific Sampling and Analyses

Habitat transect sampling (Q1)

Habitat transect surveys were used to collect wetted width, water depth, and flow velocity. We measured wetted stream width using a Nikon 8398 range finder (<1 m accuracy, range 3-200 m) at the midpoint of each mesohabitat unit (e.g. pool, riffle, run, glide). Next, using the wetted width, we selected five equally-spaced points across the midpoint of each habitat unit to measure depth (cm) and flow velocity (cm/s). Flow velocity was measured at 60% of the depth and at the substratum interface using a Marsh-McBirney Model 2000 flowmeter. From these measurements, we calculated means (water depth, flow velocity) to use in our statistical analyses (Table 2.1).

Habitat mosaic sampling (Q1)

For our habitat mosaic approach, we continuously mapped sequences of four mesohabitats (pool, riffle, run, and glide) for 3 km at each of the study sites. For safety, the starting point for sampling was 100 m downstream of the dam (at dammed sites). To quantify mesohabitat, we kayaked from upstream to downstream and identified, measured, and mapped the number, location, and size of mesohabitats along the mainstem. We identified discrete mesohabitats through agreement by two independent observers, based on an objective series of surface flow, channel morphology, and sediment composition criteria (Bisson et al., 1981; McCain et al., 1990; Harvey and Clifford, 2009). Mesohabitats were quantified using trackplots at 5-s intervals and waypoints at the upper and lower boundary for each habitat unit from a handheld Garmin GPSmap76Cx (Garmin International, Olathe, KS). Trackplots and waypoints for each sample site were imported into ArcGIS v. 10.2 (ESRI, Redlands, CA). Mesohabitat

units at each site were digitized into polygons in ArcGIS and stored as separate feature classes in the geodatabase. Each polygon layer was converted to raster format to visualize the habitat mosaic for each of the ten sample sites.

Creating habitat mosaic variables (Q1)

We used landscape ecology methods (Palmer et al., 2000; Wiens, 2002), calculated in FRAGSTATS 4.1 (McGarigal et al., 2012), to quantify the spatial heterogeneity created by the mosaic of mesohabitats. Each ArcGIS planform map was converted from a polygon-based feature file to a raster format and inputted into FRAGSTATS. Specifically, at each 3-km site, we calculated: 1) habitat diversity, 2) number of mesohabitat patches, 3) proportion of each mesohabitat, and 4) mean area of each mesohabitat at three different scales (patch-level, class-level, landscape-level; Table 2.1). In this study, patches equate to individual mesohabitats, classes represent each mesohabitat type, and landscape corresponds to each of our ten sample sites.

Habitat diversity was calculated as Shannon's Diversity Index (McGarigal and Marks, 1995), an ecologically meaningful spatial heterogeneity index that has been used in other aquatic systems (Yarnell, 2005; Yarnell et al., 2006; Drakou et al., 2009). Habitat diversity incorporates both evenness (distribution of areas between patch types) and richness (number of patch types) to determine the overall diversity of patch types. Number of patches at each site and the proportion of mesohabitat at each site were calculated to evaluate whether mesohabitat composition was different below low-head dams compared to undammed sites. Number of patches and proportion of pools and riffles along the stream have been shown to influence stream biota (Barbour et al., 1999; Rashleigh et al., 2005; Rowe et al., 2009; Pyron et al., 2011). Number, area, and

proportion of specific mesohabitat types are ecologically related but provide different pieces of habitat information. For example, even if the area of riffles is larger at some sites, proportion of riffles may or may not change depending on total stream area and size/frequency of other mesohabitats.

Transect vs. mosaic habitat - data analysis (Q1; Fig. 2.1)

To examine differences between dammed and undammed sites, we used two sets of Wilcoxon signed-rank tests (for habitat transect and habitat mosaic data, respectively). The signed-rank test is a non-parametric analysis used to test differences in a response variable between two groups (here dammed and undammed sites). Boxplots helped visualize the results. In these analyses, the presence/absence of a dam was the treatment and the response variables were wetted width, water depth, flow velocity (for habitat transect data) or habitat diversity, number of mesohabitat patches, and proportion of mesohabitats (for habitat mosaic data).

Low-head dam effects on habitat variability (Q2; Fig. 2.1)

To investigate whether low-head dams altered the natural variability in stream habitat diversity across sites, we bootstrapped empirically-derived, site-specific habitat diversity measures to estimate standard deviations in habitat diversity for dammed and undammed sites. First, as described above, we used empirical estimates of abundance and distribution of mesohabitats to calculate Shannon's Diversity Index at each site. Next, we ran 99 permutations of a bootstrapping procedure. For each permutation, we calculated standard deviations of Shannon's Diversity for randomly selected empirical data from three dammed sites and three undammed sites. Finally, we used a Wilcoxon test to quantitatively compare differences in

variation in habitat diversity (standard deviation of Shannon's Diversity Index) at dammed and undammed sites.

Fish sampling

Fish were sampled using a two-person mini-Missouri trawl at 20 randomly selected mesohabitat units (five pools, five riffles, five runs, five glides) at each of the ten study sites described above. In cases where there were less than five mesohabitat units of a particular type, all units of that mesohabitat type were sampled. The mini-Missouri trawl is a two-seam slingshot balloon trawl covered with a 3.2 mm delta style mesh (Herzog et al., 2009) that can be used in wadeable and non-wadeable areas. This construction ensured consistent sampling across mesohabitats and study sites. To sample with the mini-Missouri trawl, two people pulled the trawl while wading from upstream to downstream at a speed slightly faster than current speed as is proposed by the creators of this gear. Our tows were standardized to 30 m. All captured fish were placed in an aerated live well, identified to species, enumerated, and then returned alive to the stream. Because the number and length of trawls were the same in all habitats and at all sites, fish estimates (number / trawl) were comparable. We used this fish biodiversity data set (below dams and at undammed sites) to compare habitat sampling (transect vs. mosaic) using both statistical analyses (ANCOVA vs. path analysis).

Transect vs. mosaic habitat at dammed and undammed sites (Q3; Fig. 2.1)

We used an ANCOVA to compare the effect of a categorical factor (dam-no dam) on a dependent variable (species richness) while controlling for the effect of continuous covariates

(transect and mosaic habitat metrics). Fish abundances were log transformed to satisfy parametric assumptions of this analysis.

Transect vs. mosaic habitat at dammed and undammed sites (Q4a; Fig. 2.1)

We also used path analysis to test how downstream species richness was influenced by habitat at dammed vs. undammed sites. Path analysis analyzes the complex networks of causal relationships in ecosystems (Shipley, 2002; Grace, 2006) using partial regressions to establish strengths of interactions among sets of variables while accounting for other interactions within the dataset. Standardized path coefficients (standardized β) indicate the strength of relationships and R^2 quantify the amount of variation explained by specific sets of variables. We avoided multicollinearity by removing models with high variance inflation factors (VIF) > 10 (Borcard et al., 2011). For the downstream of dam - undammed site path analysis, we used all sample sites (n = 10). Dam was the exogenous variable, habitats were the endogenous, mediated variables, and fish species richness was the response variable. We used the library lavaan with function sem in R (Rosseel, 2012).

Transect vs. mosaic habitat upstream and downstream of dams (Q4b; Fig. 2.1)

We also sampled fish and habitat for 3 km above all low-head dams using transect and mosaic approaches. Since the impounded area above the dams consisted entirely of pool habitat, we modified our sample design to ensure a complete assessment of fish biodiversity. Beginning 0.2 km upstream of the dam (for safety purposes), we sampled along transects spaced every 0.2 km to the 1 km above the dam, then every 0.5 km until we reached 3 km above the dam (except at Riverwalk Dam where the impoundment only reached 2 km above the dam). Wetted width

was collected using a Nikon 8398 range finder (<1 m accuracy, range 3-200 m) at each sample point. Depth was collected using a depth finder (Lowrance X-4 depth finder). We were unable to accurately measure flow velocity because greater depths prevented us from positioning the flowmeter at the required 60% interval. Fish were sampled using a mini-Missouri trawl attached to the bow of a jon boat with a lead line of 8 m and doors affixed to the bridle to keep the mouth of the net from tangling during deployment. Sampling occurred from upstream to downstream at a pace of ~6 km/hr for 100 m. Fish were identified to species, enumerated, and returned alive to the stream. For the upstream-downstream path analysis (Q4b), we used all dam locations (n = 5). Dam was the exogenous variable; habitats were endogenous, mediated variables, and fish species richness was the response variable. All analyses were performed using R (R Development Core Team 2013). Throughout we report p-values and clearly state comparisons made (Wasserstein & Lazar 2016).

Finally, we mapped the geomorphic dam footprint (both upstream and downstream) for the five low-head dams in our study area to depict synthetic basin-wide impacts of low-head dams on habitat. Methods for the geomorphic dam footprint calculations are described in detail elsewhere (Fencl et al., 2015).

Results

Transect vs. mosaic habitat data (Q1)

Habitat transect approach

Differences in means of habitat transect variables were relatively small downstream of dams compared to undammed sites (Fig. 2.4a-c). *Width* was the only habitat transect variable that was significantly different ($W = 2261$, $p < 0.001$; Fig. 2.4a). Specifically *width* was greater

below dams than at undammed sites. The other two habitat transect variables, *depth* ($W = 1677$, $p = 0.69$; Fig. 2.4b) and *velocity* ($W = 1552$, $p = 0.76$; Fig. 2.4c), were not significantly different between dammed and undammed sites.

Habitat mosaic approach

Differences in means of habitat mosaic variables revealed several novel results about the effects of low-head dams on stream habitat (Fig. 2.4d-f). Although we found no significant difference in mean habitat diversity below dams relative to undammed locations ($W = 15.2$, $p = 0.60$; Fig. 2.4d), the proportion of riffle ($W = 25$, $p < 0.05$; Fig. 2.4e) and area of riffle habitat ($W = 684$, $p = 0.01$; Fig. 2.4f) were significantly higher below dams compared to undammed locations. This result showed that the critical riffle habitat both increased in size and comprised a larger proportion of the total stream mosaic relative to other mesohabitats at dammed sites compared to undammed sites.

Low-head dam effects on habitat variability (Q2)

Although mean habitat diversity did not differ (Fig. 2.4d), dammed sites had less variation in stream habitat diversity than undammed sites (Fig. 2.5). Specifically, undammed sites had a significantly higher mean standard deviation in habitat diversity (i.e., more varied and more variable habitat) than dammed sites ($\chi2 = 50.57$, $p < 0.001$), such that low-head dams depressed natural variability in habitat.

Transect vs. mosaic habitat; fish biodiversity (Q3)

We captured a total of 8,033 fish representing 36 species encompassing 18 genera upstream and downstream of five low-head dam sites and five undammed sites along the UNRB (Table 2.2). Using an ANCOVA on habitat transect data, we found no significant relationship between species richness and habitat and no significant relationship between species richness and the presence of dams (Fig. 2.6a-c). Specifically, slopes were neither significantly different from zero nor different between dammed and undammed sites for species richness using width [habitat ($F = 0.05$; df = 3, 6; $p = 0.83$); dam treatment ($F = 0.01$; df = 3, 6; $p = 0.95$); Fig. 2.6a], depth [habitat ($F = 0.25$; df = 3, 6; $p = 0.64$); dam treatment ($F = 0.60$; df = 3, 6; $p = 0.47$); Fig. 2.6b], or flow velocity [habitat ($F = 0.09$; df = 3, 6; $p = 0.78$); dam treatment ($F = 1.45$; df = 3, 6; $p = 0.27$); Fig. 2.6c].

Using ANCOVA on habitat mosaic data, we found no statistical differences between dammed and undammed sites, but we did find significant habitat-fish relationships (Fig. 2.6d-f). Increases in habitat diversity [habitat ($F = 9.81$; df = 3, 6; $p = 0.02$); dam treatment ($F = 0.52$; df = 3, 6; $p = 0.50$); Fig. 2.6d], and proportion of riffle habitat [habitat ($F = 10.92$; df = 3, 6; $p = 0.02$); dam treatment ($F = 0.48$; df = 3, 6; $p = 0.52$); Fig. 2.6e] increased fish species richness. Proportion of pool habitat marginally decreased species richness [habitat ($F = 4.56$; df = 3, 6; $p = 0.08$); dam treatment ($F = 0.18$; df = 3, 6; $p = 0.68$); Fig. 2.6f].

Transect vs. mosaic habitat at dammed and undammed sites (Q4a)

Habitat transect data - below dams

No significant, mediated effects of low-head dams on fish species richness were detected using habitat transect data (Fig. 2.7a). Specifically, using path analysis, dams affected the habitat

transect variable, width, in that wider stream channels occurred downstream of dams ($R^2 = 0.11$; $p < 0.001$; left and middle columns). However, dam-related width changes did not significantly influence fish species richness (Fig. 3.7a; middle and right columns). Depth and velocity were inversely proportional to species richness ($R^2 = 0.07$; $p < 0.05$; Fig. 2.7a, middle and right columns), but were not significantly different between dammed and undammed sites (Fig. 2.7a; left and middle columns).

Habitat mosaic data - below dams

Path analysis revealed strong and significant mediated effects of low-head dams on species richness using habitat mosaic data (Fig. 2.7b). Sites below low-head dams had significantly higher proportions of riffle habitat ($R^2 = 0.33$; $p < 0.03$, Fig. 2.7b, left and middle columns), and strong and positive relationships also existed between the proportion of riffle habitat and fish species richness ($R^2 = 0.85$; $p < 0.001$, Fig. 2.7b, middle and right columns). Habitat diversity and proportion of pool were related to species richness (Fig 2.7b, middle and right columns), but were not consistently different between dammed and undammed sites (Fig. 2.7b, left and middle columns).

Transect vs. mosaic habitat upstream and downstream of low-head dams (Q4b)

Path analysis also detected differences in fish biodiversity among sites upstream and downstream of dams using habitat mosaic but not habitat transect data. Low-head dams reduced fish biodiversity directly ($R^2 = 0.96$; $p < 0.001$; Fig. 2.7c; bottom solid arrow). Low-head dams also reduced fish species diversity through an increase in the mediated habitat variable,

proportion of pool, above the dam ($R^2 = 0.73$; $p < 0.001$; Fig. 2.7c; top arrows left, middle, right columns).

Basin-wide dam impacts

Downstream dam-impacts on habitat extended < 2 km (Fig. 2.8 – red lines), but the geographic extent of upstream low-head dam impacts on habitat was greater (2-14 km; Fig. 2.8 – yellow lines). Together upstream and downstream dam effects had a basin-wide impact much greater than that suggested by the dam barriers alone. For example, in the UNRB, 17% of the basin area was affected by upstream or downstream dam habitat alterations (Fig. 2.8).

Discussion

The mosaic approach provided new information about changes in habitat and fish biodiversity downstream of low-head dams. By incorporating the separate and combined effects of both common and uncommon habitats, the mosaic approach generated a new type of ecologically-meaningful habitat variable (e.g., habitat diversity, number, size, proportion of habitats). Mosaic habitat variables detected the interacting nature of habitat patches, which can benefit biological conservation in aquatic ecosystems that contain low-head dams. For example, a mosaic approach revealed that both overall area of riffle habitat and the proportion of riffle increased downstream of low-head dams. The behavior of these two different, but related, mosaic metrics indicated that, at dams, riffles increased in size and also increased in proportion to other stream mesohabitats. In contrast, for our transect data, only stream width (created by scour created below the low-head dams) was significantly different between dammed and undammed sites. Riffles can be keystone habitats that promote greater overall habitat diversity

and fish biodiversity in prairie streams (Hitchman Chapter 1). Thus, our use of the mosaic approach identified the importance of this mesohabitat within the context of the adjacent mesohabitats that comprise the stream mosaic.

Another insight that our use of the mosaic approach identified was that low-head dams consistently dampened variation in habitat diversity associated with free-flowing lotic ecosystems. Habitat variability is essential for the structure and function of ecological systems and the patterns of biodiversity (Poff et al., 1997; Naiman et al., 2008). Sampling meaningful variability that drives biodiversity patterns remains challenging for field biologists, but is essential for ecosystem function (Puckridge et al., 1998; Naiman et al., 2008). Ours is not the only study to document a decrease in environmental variability due to large and small dams. For example, the Colorado River in northern Arizona was historically a turbid system with extremely variable thermal and flow fluctuations including periodic, large-scale flood events. After Glen Canyon Dam was built, however, the Colorado River became clear and cold with near-zero, long-term flow variability (i.e., flatline hydrograph; Stevens et al., 1995). Our approach yielded some interesting insights about habitat diversity across scales. Interestingly, though habitat diversity increased below low-head dams (α diversity; Whittaker, 1972), there was a dramatic and larger decrease in habitat diversity above low-head dams (β diversity; Whittaker, 1972). This leads to an overall decrease in habitat diversity at a regional scale (γ diversity; Whittaker, 1972). For environmental professionals seeking to conserve aquatic systems with and without dams, methods that capture site-to-site variability are critical because researchers and managers will fail to detect important disturbances and subsequent recovery if natural variability is not monitored.

Path analysis provided a third insight into dam-habitat-fish biodiversity relationships. Specifically, our path analysis on habitat mosaic data showed that a change in a specific

component of habitat diversity (proportion of riffle), not just habitat diversity in general, was the functional link between low-head dams, habitat, and fish biodiversity. In the Qingyi River, China, low-head dams also modify local habitat characteristics (e.g. substrate heterogeneity) above and below low-head dams and alter fish species richness, but, in this study, using linear regression, the link between dams, species richness and substrate heterogeneity was only inferred (Li et al., 2016). Elsewhere, for non-dam disturbances, mediated effects have been shown to significantly alter aquatic communities. For example, Santin and Willis (2007) found that breakwaters indirectly influence fish communities by altering physical habitat. Our finding that low-head dams affected fish biodiversity indirectly through alterations in habitat is important and can easily be included in future dam-related statistical analyses.

Using path analysis and metrics derived from habitat mosaic data, we also confirmed that impounded pool habitat upstream of low-head dams reduced fish biodiversity. In our research and elsewhere, the impounded area upstream of low-head dams increased water depth, decreased current velocity, reduced substrate size, and decreased fish assemblages (Gillette et al., 2005; Poulet, 2007; Yan et al., 2013). The adverse upstream geomorphic footprints of our five Neosho low-head dams extended over five times the area of downstream habitat alterations (Fencl et al., 2015). Even though there was an increase in species richness below low-head dams due to increased riffle proportion, the dramatic and more extensive decrease in species richness above the dams confirmed that low-head dams are a major disturbance in flowing water systems. To understand and manage how the *anthroposphere* (human impacts related to dams) impacts the *hydrosphere* (stream habitat) and *biosphere* (native biodiversity) both upstream and downstream effects need to be considered for both individual dams and all dams within a basin.

Finally, all of our analyses considered together have clarified aspects of the complex relationship among low-head dams and their influence on stream habitat and fish biodiversity. Specifically, we have shown that dams, habitat, and fish need to be examined as an integrated series of related effects. Looking at the isolated effect of dams on habitat and the isolated effects of habitat on fish were informative but revealed only part of the story. Specifically, examining mosaic habitat at dammed and undammed sites showed that lowhead dams affected mean *proportion of riffle*, mean *riffle area*, and variability in *habitat diversit*y (Fig. 2.4, 2.5). The ANCOVA analysis, which examined how habitat affected fish diversity at dammed and undammed sites, showed that *habitat diversity*, *proportion* of *riffle*, and *proportion of pool* affected fish richness although these variables were not different at dammed and undammed site (Fig. 6). The real discovery was gained from concurrently examining the effects of dams on fish as mediated by habitat (i.e., path analysis). The path analysis integrated discrepancies among individual analyses by showing that *habitat diversity*, *proportion of riffle, proport*ion *of pool* affected fish richness, but only *proportion* of *riffle* was both affected by dams (Fig. 7b), and, in turn, affected fish richness. This finding about the need to statistically address dam-habitat-fish together is an important consideration for future studies that seek to conserve fragmented aquatic ecosystems.

Our study highlighted the value of habitat mosaics, an approach that quantified composition and configuration for both common and uncommon habitats. The mosaic approach is no more time intensive or expensive than transect sampling. For example, we were able to continuous map riverine habitats using little more than a kayak and a GPS unit. The mosaic approach has broad applicability to other ecosystems with the increasing availability of spatially explicit models and geographic information systems. Also, we found path analysis was a useful

tool for examining low-head dam effects on fish biodiversity as mediated through alterations to habitat. Although use of mediated statistical effects is presently rare in low-head dam studies, this statistical approach can be widely incorporated into future dam-habitat-biodiversity studies. Thus, mosaic habitat sampling and path analysis will help conservation practitioners to construct and implement better science-based management plans and sampling regimes for disturbed and degraded aquatic systems worldwide.

References

Barbour, M.T., Gerritsen, J., Snyder, B.D., Stribling, J.B., 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish, second edition. EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, D.C.

Beatty, S., Allen, M., Lymbery, A., Jordaan, M.S., Morgan, D., Impson, D., Marr, S., Ebner, B., Weyl, O.L.F., 2017. Rethinking refuges: Implications of climate change. Biological Conservation. 209, 188-195.

Bellmore, J.R., Duda, J.J., Craig, L.S., Greene, S.L., Torgersen, C.E., Collins, M.J., Vittum, K., 2016. Status and trends of dam removal research in the United States. Wiley Interdisciplinary Reviews: Water, 4. DOI: 10.1002/wat2.1164.

Benstead, J.P., March, J.G., Pringle, C.M., Scatena, F.N., 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. Ecological Applications. 9, 656-668.

Bisson, P.A., Nielsen, J.L., Palmason, R.A., Grove, L.E., 1981. A system of naming habitat in small streams, with examples of habitat utilization by salmonids during low streamflow, in: Armantrout, N.B. (Ed), Acquisition and Utilization of Aquatic Habitat Inventory Information. Proceedings of a symposium, Oct. 28-30, 1981, Portland, Oregon. Hagen Publishing Co., Billings, Montana, pp. 62-73.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical ecology with R. Springer, New York, New York, USA.

Bruder, A., Salis, R.K., Jones, P.E., Matthaei, C.D., 2017. Biotic interactions modify multiple-stressor effects on juvenile brown trout in an experimental stream food web. Global

Change Biology.

http://onlinelibrary.wiley.com.er.lib.kstate.edu/doi/10.1111/gcb.13696/epdf.

Cheek, B.D., Grabowski, T.B., Bean, P.T., Groeschel, J.R., Magnelia, S.J., 2016. Evaluating

habitat associations of a fish assemblage at multiple spatial scales in a minimally

disturbed stream using low-cost remote sensing. Aquatic Conservation: Marine and

Freshwater Ecosystems. 26, 20-34.

Cheng, S.T., Herricks, E.E., Tsai, W.P., Chang, F.J., 2016. Assessing the natural and

anthropogenic influences on basin-wide fish species richness. Science of the Total

Environment. 572, 825-836.

Chick, J.H., Pegg, M.A., Koel, T.M., 2006. Spatial patterns of fish communities in the Upper

Mississippi River System: Assessing fragmentation by low-head dams. River Research

and Applications. 22, 413-427.

Chu, L., Wang, W., Zhu, R., Yan, Y., Chen, Y., Wang, L., 2015. Variation in fish assemblages

across impoundments of low-head dams in headwater streams of the Qingyi River,

China: effects of abiotic factors and native invaders. Environmental Biology of Fishes.

98, 101-112.

Cooper, A.R., Infante, D.M., Daniel, W.M., Wehrly, K.E., Wang, L., Brenden, T.O., 2017.

Assessment of dam effects on streams and fish assemblages of the conterminous USA.

Science of the Total Environment. 586, 879-889.

Csiki, S.R., Rhoads, B.L., 2010. Hydraulic and geomorphological effects of run-of-river dams.

Progress in Physical Geography. 34, 755–780.

Dodd, H.R., Hayes, D.B., Baylis, J.R., Carl, L.M., Goldstein, J.D., McLaughlin, R.L., Noakes,

D.L.G., Porto, L.M., Jones, M.L. 2003. Low-head sea lamprey barrier effects on stream

habitat and fish communities in the Great Lakes basin. Journal of Great Lakes Research. 29, 386-402.

Drakou, E.G., Bobori, D.C., Kallimanis, A.S., Mazaris, A.D., Sgardelis, S.P., Pantis, J.D., 2009. Freshwater fish community structured more by dispersal limitation than by environmental heterogeneity. Ecology of Freshwater Fish. 18, 369-379.

Fencl, J.S., Mather, M.E., Costigan, K.H., Daniels, M.D., 2015. How big of an effect do small dams have? using geomorphological footprints to quantify spatial impact of low-head dams and identify patterns of across-dam variation. Plos One. 10, e0141210.doi:10.1371/journal.pone.0141210.

Fencl J. S., M. E. Mather, J. M. Smith, and S. M. Hitchman. 2017. The blind men meet the elephant at the dam: alternative spatial and taxonomic components reveal different insights about how low-head dams impact fish biodiversity. Ecosphere (in press).

Fitzpatrick, F.A., Waite, I.R., D'Arcte, P.J., Meador, M.R., Maupin, M.A., Gurtz, M.E., 1998. Revised methods for characterizing stream habitat in the national water quality assessment program. WRI Report 98-4052. U.S. Geological Survey, Raleigh, N.C.

Gillette, D.P., Tiemann, J.S., Edds, D.R., Wildhaber, M.L. 2005. Spatiotemporal patterns of fish assemblage structure in a river impounded by low-head dams. Copeia. 3, 539-549.

Grace, J.B., 2006. Structural equation modeling and natural systems. Cambridge University Press, New York.

Graf, W.L., 1993. Landscapes, commodities, and ecosystems: The relationship between policy and science for American river, in: Water Science and Technology Board, National Research Council. Sustaining Our Water Resource. Washington, D.C. National Academy Press, pp.11-42.

Greathouse, E.A., Pringle, C.M., McDowell, W.H., Holmquist, J.G., 2006. Indirect upstream

effects of dams: Consequences of migratory consumer extirpation in Puerto Rico.

Ecological Applications. 16, 339-352.

Harvey, G.L., Clifford, N.J., 2009. Microscale hydrodynamics and coherent flow structures in

rivers: Implications for the characterization of physical habitat. River Research and

Applications. 25, 160-180.

Hauer, F.R., Lamberti, G.A., 2007. Methods in Stream Ecology. 2nd ed. Elsevier, Burlington,

Massachusetts, USA.

Hastings, R.P., Meiners, S.J., Colombo, R.E., Thomas, T.E. 2016. Contrasting impacts of dams

on the metacommunity structure of fish and macroinvertebrate assemblages. North

American Journal of Fisheries Management. 36, 1358-1367.

Helfrich, L.A., Liston, C., Hiebert, S., Albers, M., Frazer, K., 1999. Influence of low-head

diversion dams on fish passage, community composition, and abundance in the

Yellowstone River, Montana. Regulated Rivers: Research and Management. 7, 21–32.

Helms, B.S., Werneke, D.C., Gangloff, M.M., Hartfield, E.E., Feminella, J.W., 2011. The

influence of low-head dams on fish assemblages in streams across Alabama. Journal of

the North American Benthological Society. 30, 1095-1106.

Herzog, D.P., Ostendorf, D.E., Hrabik, R.A., Barko, V.A., 2009. The mini-Missouri trawl: a

useful methodology for sampling small-bodied fishes in small and large river systems.

Journal of Freshwater Ecology. 24, 103-108.

Hitchman, S.M., Mather, M.E., Smith, J.M., Fencl, J.S., 2017. Identifying keystone habitats with

a mosaic approach can improve biodiversity conservation in disturbed ecosystems.

Global Change Biology. https://doi.org/10.1111/gcb.13846.

Jowett, I.G., 1993. A method for objectively identifying pool, run, and riffle habitats from

    physical measurements. New Zealand Journal of Marine and Freshwater Research. 27,

    241-248.

Juracek, K.E., Perry, C.A., 2005. Gravel sources for the Neosho River in Kansas, 2004. United

    States Geological Survey Scientific Investigations Report 2005–5282.

Krause, J.R., Bertrand, K.N., Kafle, A., Troelstrup, N.H., Jr., 2013. A fish index of biotic

    integrity for South Dakota's Northern Glaciated Plains Ecoregion. Ecological Indicators.

    34, 313-322.

Li, X., Li, Y.R., Chu, L., Zhu, R., Wang, L.Z., Yan, Y.Z., 2016. Influences of local habitat,

    tributary position, and dam characteristics on fish assemblages within impoundments of

    low-head dams in the tributaries of the Qingyi River, China. Zoological Research. 37, 67-

    74.

Lowe, W.H., Likens, G.E., Power, M.E., 2006. Linking scales in stream ecology. Bioscience. 56,

    591-597.

Lyons, J., 1992. The length of stream to sample with a towed electrofishing unit when fish

    species richness is estimated. North American Journal of Fisheries Management. 12, 198-

    203.

McCain, M., Fuller, D., Decker, L., Overton, K., 1990. Stream habitat classification and

    inventory procedures for northern California. FHC Currents. No.1. U.S. Department of

    Agriculture. Forest Service, Pacific Southwest Region.

McGarigal, K., Marks, B.J., 1995. FRAGSTATS. Spatial Analysis Program for Quantifying

    Landscape Structure. General Technical Report PNW-GTR-351. USDA Forest Service.

McGarigal, K., Cushman, S., Ene, E., 2012. FRAGSTATS V4: Spatial pattern analysis program for categorical and continuous maps, computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Naiman, R.J., Latterell, J.J., Pettit, N.E., Olden, J.D., 2008. Flow variability and the biophysical vitality of river systems. Comptes Rendus Geoscience. 340, 629-643.

Palmer, M.A., Swan, C.M., Nelson, K., Silver, P., Alvestad, R., 2000. Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. Landscape Ecology. 15, 563-76.

Pichon, C.L., Tales, E., Gorges, G., Baudry, J., Boet, P., 2016. Using a continuous riverscape survey to examine the effects of the spatial structure of functional habitats on fish distribution. Journal of Freshwater Ecology. 31, 1-19.

Platts, W.S., Megahan, W.F., Minshall, G.W., 1983. Methods for evaluating stream, riparian, and biotic conditions. Ogden, UT, USA: US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. General Technical Report INT-138.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime. Bioscience. 47, 769-784.

Poff, N.L., Hart, D.D., 2002. How dams may vary and why it matters for the emerging science of dam removal. Bioscience. 5, 659–668.

Poulet, N., 2007. Impact of weirs on fish communities in a piedmont stream. River Research and Applications. 23, 1038-1047.

Pringle, C.M., Naiman, R.J., Bretschko, G., Karr, J.R., Oswood, M.W., Webster, J.R., Welcomme, R.L., Winterbourn, M.J., 1988. Patch dynamics in lotic systems: The stream

as a mosaic. Journal of the North American Benthological Society. 7, 503-524.

Puckridge, J.T., Sheldon, F., Walker, K.F., Boulton, A.J., 1998. Flow variability and the ecology of large rivers. Marine and Freshwater Research. 49, 55-72.

Pyron, M., Williams, L., Beugly, J., Jacquemin, S.J., 2011. The role of trait-based approaches in understanding stream fish assemblages. Freshwater Biology. 56, 1579-1592.

R Core Development Team. 2013. R: A language and environment for statistical computing. R foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/.

Rahel, F.J., 2007. Biogeographic barriers, connectivity, and biotic homogenization: It's a small world after all. Freshwater Biology. 52, 696–710.

Rashleigh, B., Parmar, R., Johnston, J.M., Barber, M.C., 2005. Predictive habitat models for the occurrence of stream fishes in the mid-Atlantic highlands. North American Journal of Fisheries Management. 25, 1353-1366.

Rosseel, Y., 2012. lavaan: An R package for structural equation modeling. Journal of Statistical Software. 48, 1–36.

Rowe, D.C., Pierce, C.L., Wilton, T.F., 2009. Fish assemblage relationships with physical habitat in wadeable Iowa streams. North American Journal of Fisheries Management. 29, 1314-1332.

Santin, S., Willis, T.J., 2007. Direct versus indirect effects of wave exposure as a structuring force on temperate cryptobenthic fish assemblages. Marine Biology. 151, 1683-1694.

Santucci, V.J., Gephard, S.R., Pescitelli, S.M., 2005. Effects of multiple low-head dams on fish, macroinvertebrates, habitat, and water quality in the Fox River, Illinois. North American Journal of Fisheries Management. 25, 975-992.

Shipley, B., 2002. Cause and correlation in biology: a user's guide to path analysis, structural

    equations and causal inference. Cambridge University Press, Cambridge.

Simonson, T.D., Lyons, J., Kanehl, P.D., 1994. Quantifying fish habitat in streams: transect

    spacing, sample size, and a proposed framework. North American Journal of Fisheries

    Management. 14, 607–615.

Slawski, T.M., Veraldi, F.M., Pescitelli, S.M., Pauers, M.J., 2008. Effects of tributary spatial

    position, urbanization, and multiple low-head dams on warmwater fish community

    structure in a Midwestern stream. North American Journal of Fisheries Management. 28,

    1020-1035.

Smith, J.M., Mather, M.E., 2013. Beaver dams maintain native fish biodiversity by increasing

    habitat heterogeneity throughout a low-gradient stream network. Freshwater Biology. 58,

    1523-1538.

Stevens, L.E., Schmidt, J.C., Ayers, T.J., Brown, B.T., 1995. Flow regulation, geomorphology,

    and Colorado River marsh development in the Grand Canyon, Arizona. Ecological

    Applications. 5, 1025-1039.

Taka, M., Aalto, J., Virkanen, J., Luoto, M., 2016. The direct and indirect effects of watershed

    land use and soil type on stream water metal concentrations. Water Resources Research.

    52, 7711-7725.

Tiemann, J.S., Gillette, D.P., Wildhaber, M.L., Edds, D.R., 2004. Effects of lowhead dams on

    riffle-dwelling fishes and macroinvertebrates in a Midwestern river. Transactions of the

    American Fisheries Society. 133, 705-717.

Tonra, C.M., Sager-Fradkin, K., Morley, S.A., Duda, J.J., Marra, P.P., 2015. The rapid return of

    marine-derived nutrients to a freshwater food web following dam removal. Biological

Conservation. 192, 130-134.

Tullos, D.D., Collins, M.J., Bellmore, J.R., Bountry, J.A., Connolly, P.J., Shafroth, P.B., Wilcox, A.C., 2016. Synthesis of common management concerns associated with dam removal. Journal of the American Water Resources Association. 52, 1179-1206.

Ward, J.V., Stanford, J.A., 1979. The ecology of regulated streams. Plenum, New York.

Wasserstein, R. L., Lazar, N. A., 2016. The ASA's statement on P-values: context, process, and purpose. The American Statistician. 70, 129–133.

Watters, G.T., 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoidia) and their hosts. Biological Conservation. 75, 79-85.

Weaver, D.M., Kwak, T.J., Pollock, R.H., 2014. Sampling characteristics and calibration of snorkel counts to estimate stream fish populations. North American Journal of Fisheries Management. 34, 1159-1166.

Whittaker, R. H. 1972. Evolution and Measurement of Species Diversity. Taxon. 21, 213-251.

Wiens, J.A., 2002. Riverine landscapes: taking landscape ecology into the water. Freshwater Biology. 47, 501-15.

Yan, Y.Z., Wang, H., Zhu, R., Chu, L., Chen, Y.F., 2013. Influences of low-head dams on the fish assemblages in the headwater streams of the Qingyi watershed, China. Environmental Biology of Fishes. 96, 495-506.

Yarnell, S.M., 2005. Spatial heterogeneity of *Rana boylii* habitat: physical processes, quantification and ecological meaningfulness. PhD dissertation, University of California, Davis.

Yarnell, S.M., Mount, J.F., Larsen, E.W., 2006. The influence of relative sediment supply on riverine habitat heterogeneity. Geomorphology. 80, 310-324.

Yeiser, J.M., Richter, S.M., 2015. Microhabitat conditions influence mesohabitat associations and distribution of larval salamanders in headwater streams. Hydrobiologia. 751, 175-187.

Figure 2.1. Conceptual diagram illustrating how our research tests alternate approaches to habitat sampling and statistical analyses, which can alter stream habitat and fish biodiversity. Our four specific research questions are indicated.
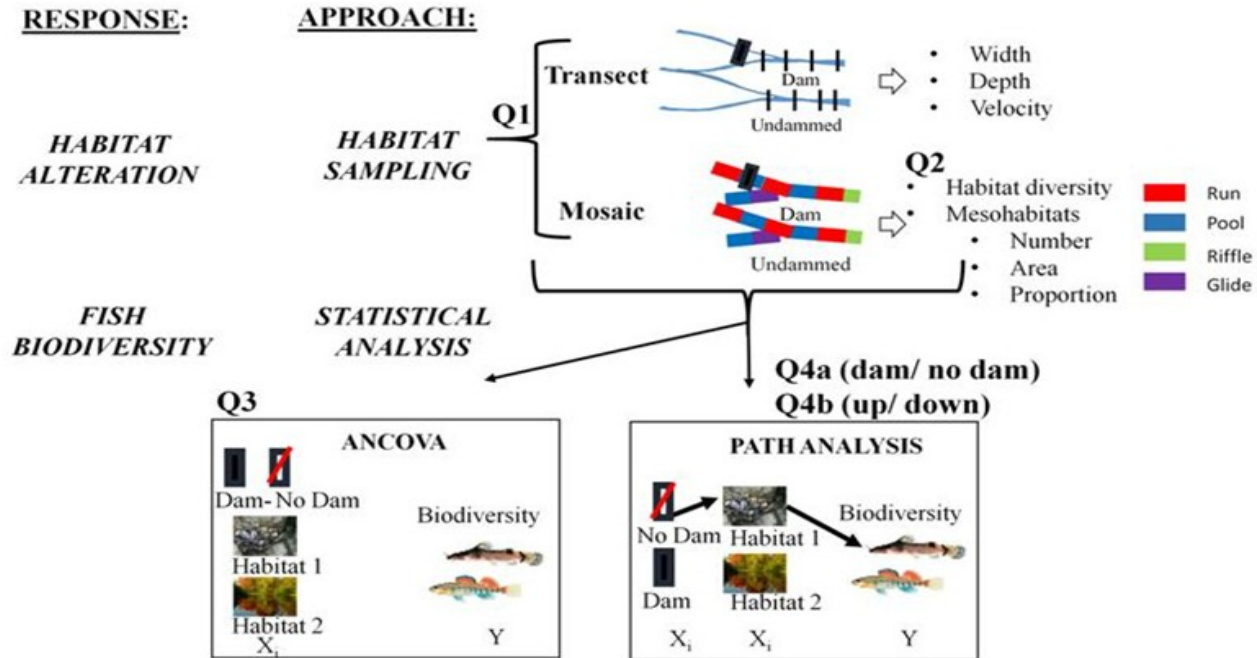
Figure 2.2. Map of study area including (a) Neosho River within the state of Kansas, and (b) 10 3-km sampling sites within the Upper Neosho River basin along the Neosho and Cottonwood Rivers, KS, below five low-head dam sites and at five undammed sites.
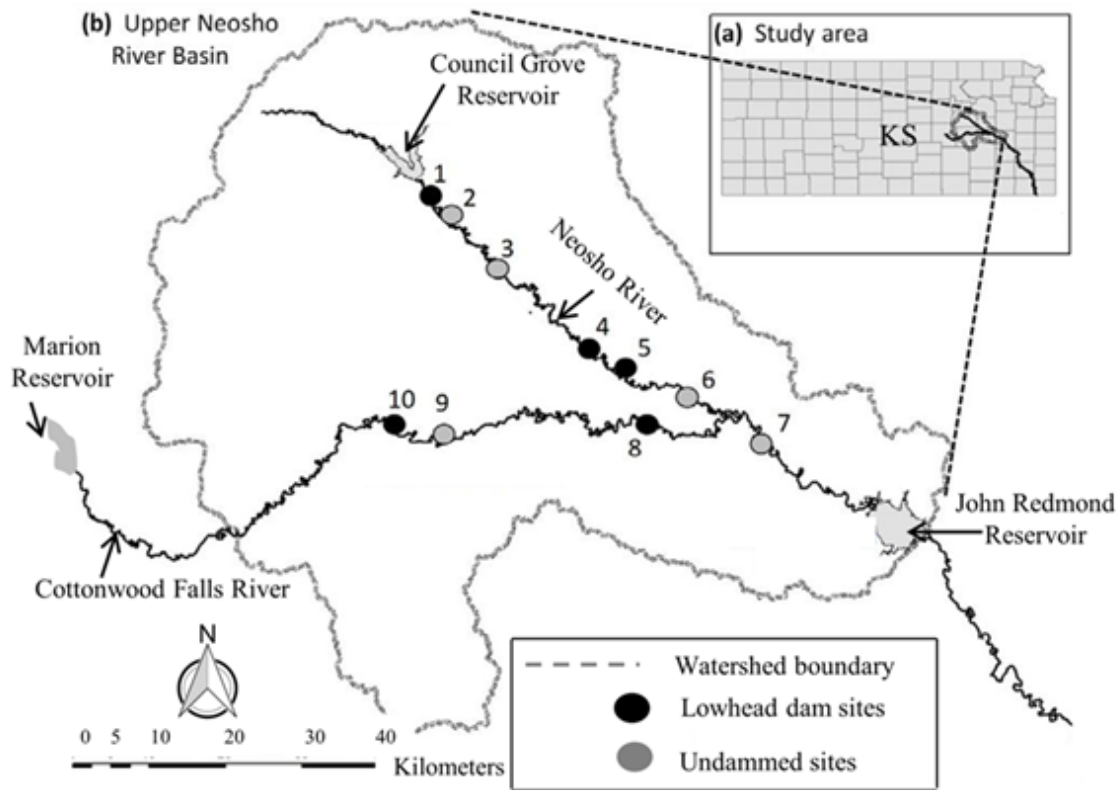
Figure 2.3. Horizontal stacked bar plot of the relative proportion of mesohabitats (pool, riffle, run, and glide) at five dammed (D) and five undammed (U) sites along the Neosho and Cottonwood Rivers, KS. Sample sites are numbered as shown in Fig. 3-2.
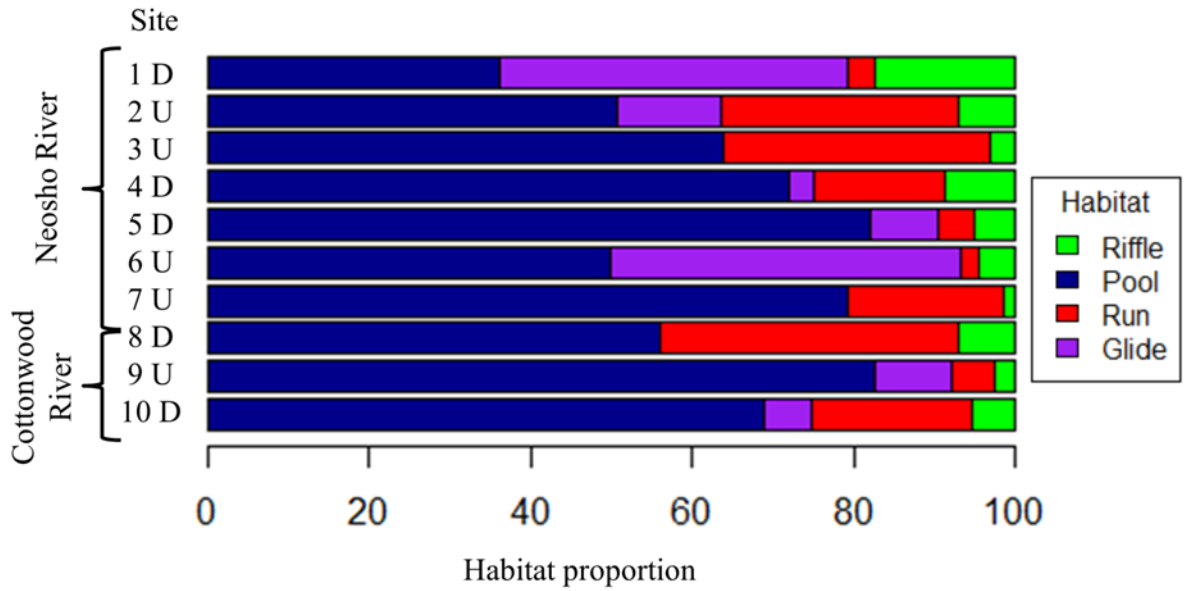
Figure 2.4. Boxplots showing six habitat variables (a-f) at dammed (downstream) and undammed sampling sites. Habitat data were collected using both (a-c) transect and (e-f) mosaic approaches. Data are means +/- 1 SE. P values are presented for significant relationships.
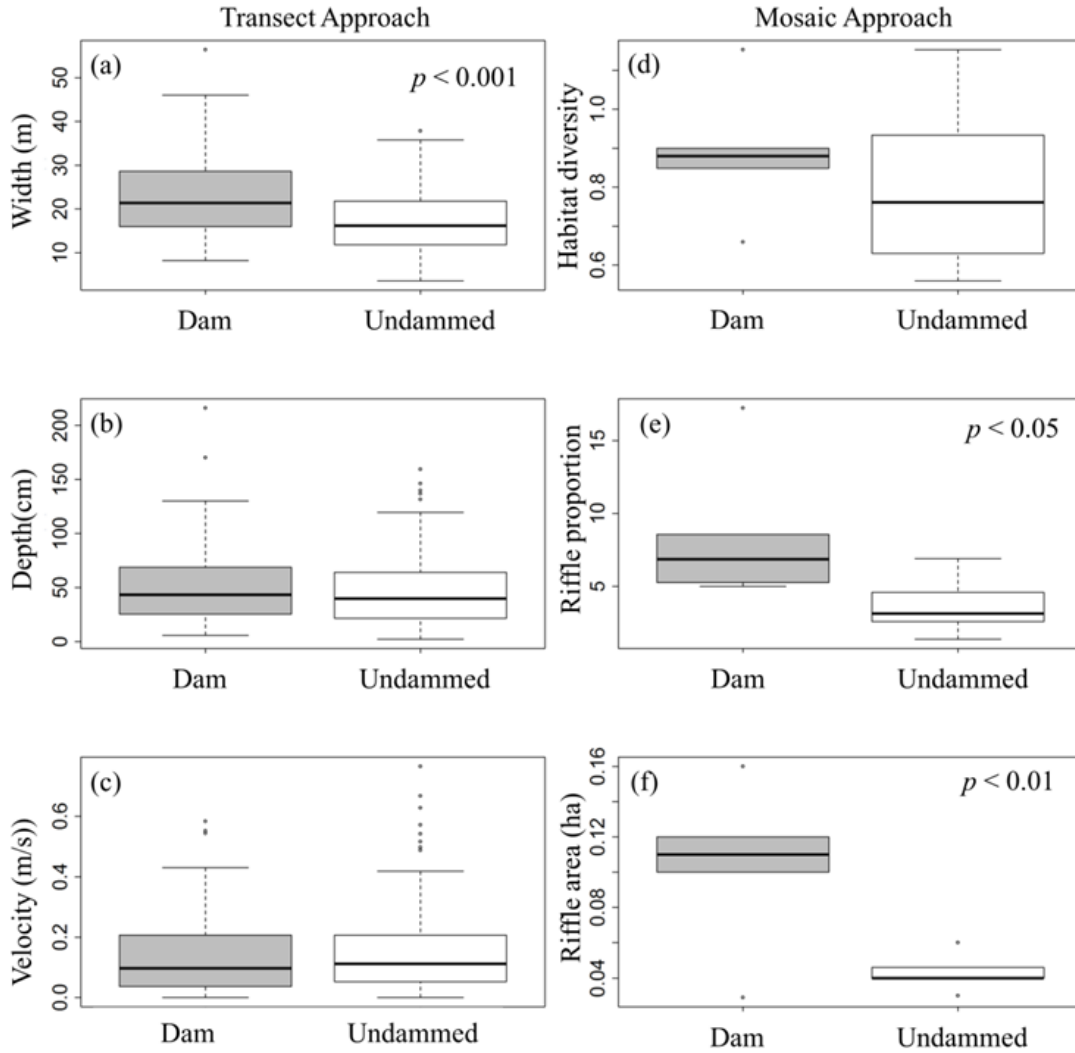
Figure 2.5. Comparison of standard deviation in habitat diversity at dammed (downstream) and undammed sites. Data are the result of a bootstrapping procedure designed to quantify variation in habitat diversity. Data are means +/- 1 SE.
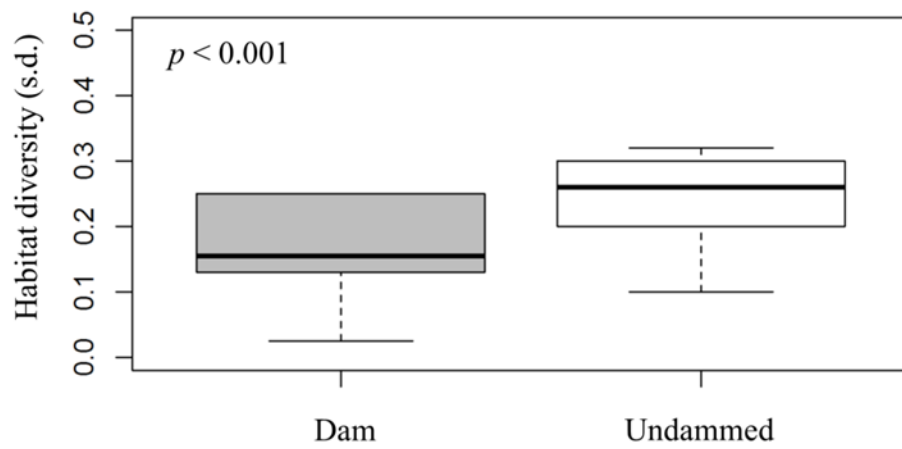
Figure 2.6. Regression plots depicting results of an ANCOVA analysis examining the relationship between species richness and habitat at dammed (downstream) and undammed sites. Habitat data were collected using (a-c) transect and (e-f) mosaic approaches. R^2 and p values are presented for significant relationships.
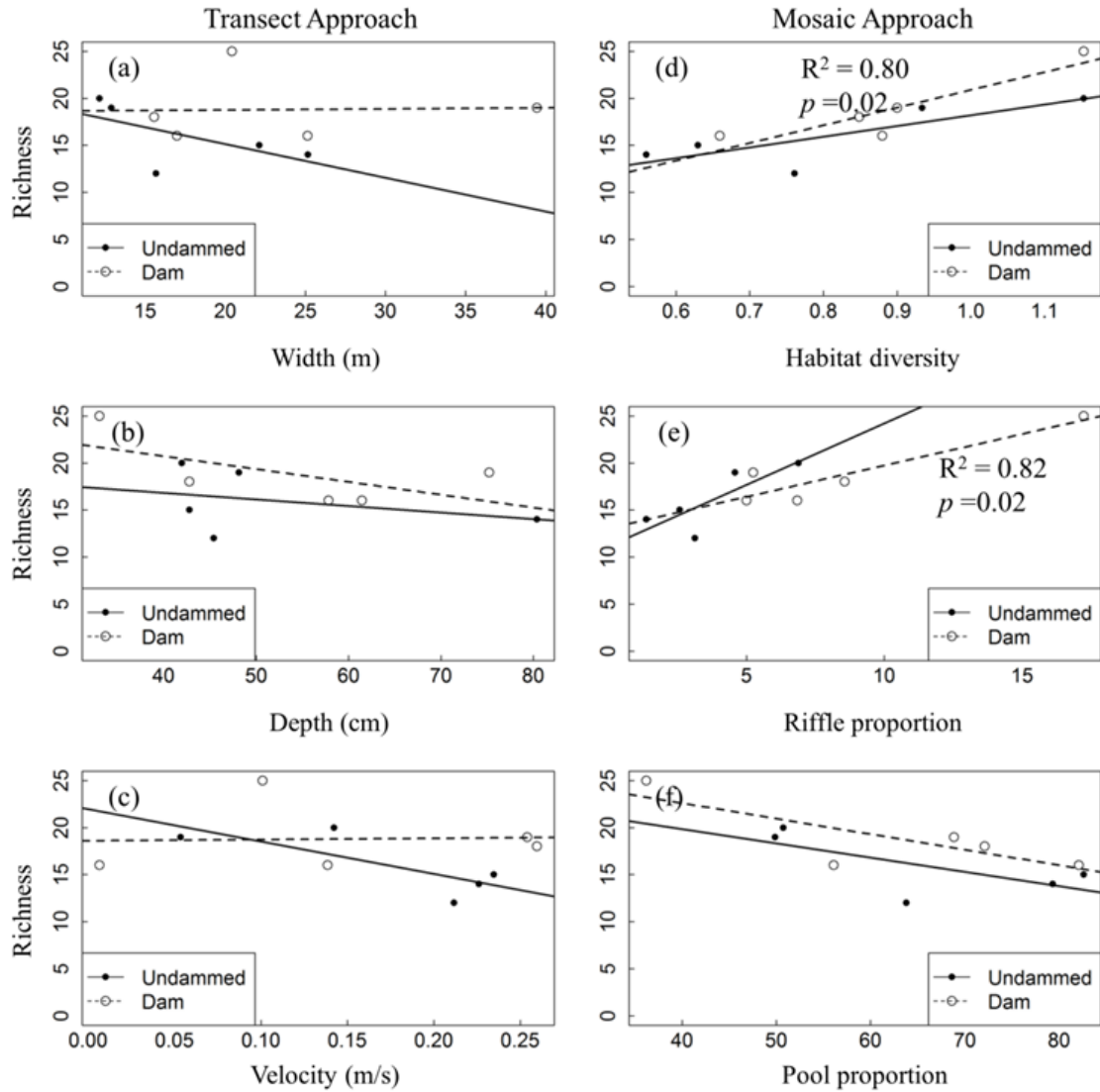
Figure 2.7. Path analyses for species richness at (a) dammed (downstream) versus undammed locations using habitat transect data, (b) dammed (downstream) versus undammed locations using habitat-mosaic data and (c) the upstream vs. downstream effects of low-head dams using habitat mosaic data. Due to high collinearity, proportion of pool habitat was the only variable used in the upstream-downstream model. We only show significant relationships at α = 0.05. Solid lines represent positive relationships and dashed lines represent negative relationships. The standardized slope (β), coefficient of determination (R^2), and significance (p) are shown for each variable pair (i.e., over each connecting line).
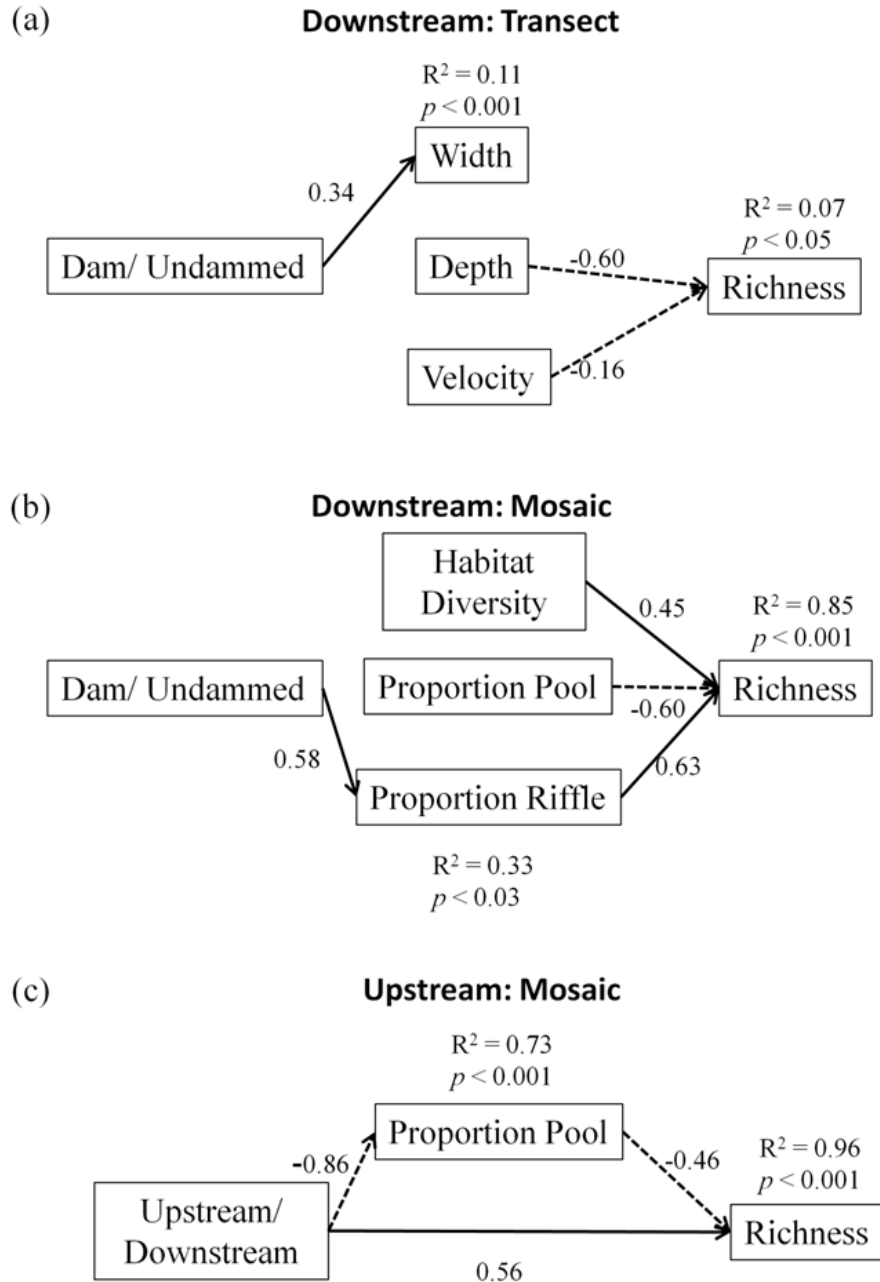
Figure 2.8. Map showing upstream (yellow tracks) and downstream (red tracks) geomorphic dam footprints at five low-head dams in the Upper Neosho River basin. The five inserts represent our five dam study sites. The maps indicate upstream and downstream dam footprints which comprise a substantial component (17%) of the Upper Neosho River basin.
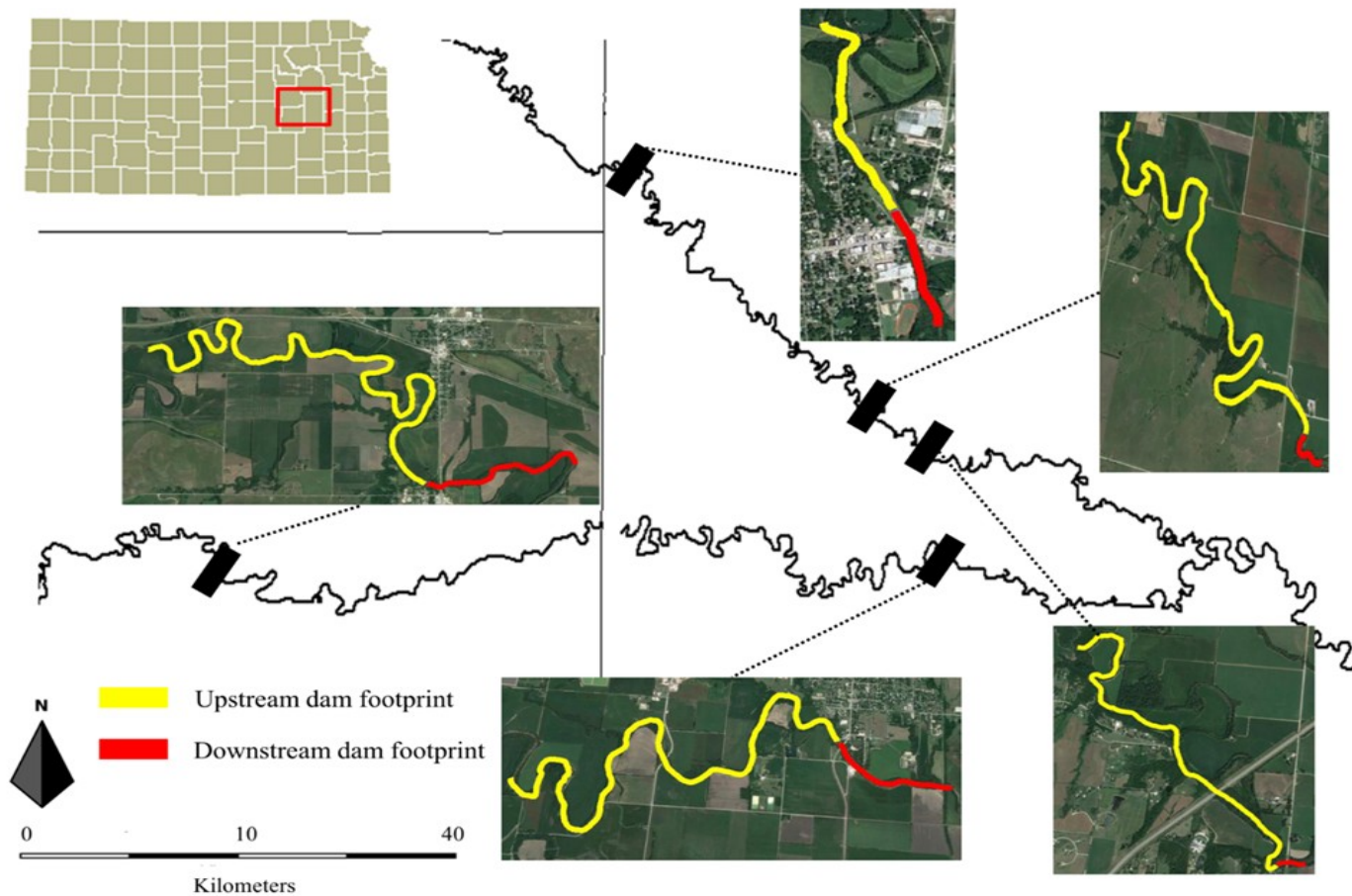
Table 2.1. Summary of stream habitat measurements taken from the Upper Neosho River Basin and used in statistical analyses.

Approach	Metrics	Description	Range	StDev
Transect				
	Width (m)	Wetted width during baseflow conditions	3.6-56.4	9.9
	Depth (m)	Mean depth at 5 equally-spaced points	0.02-2.16	0.42
	Flow Velocity (m/s)	Mean flow velocity at 5 equally-spaced points	0-0.8	0.17
Mosaic				
	Habitat diversity	Shannon's habitat diversity index (H')	0.6-1.2	15.66
	Number of patches	Number of overall mesohabitat patches	17-59	13.17
	Proportion riffle	Proportion of riffle habitat at each site	1.4-17.2	4.46
	Proportion pool	Proportion of pool habitat at each site	36.2-82.6	15.66
	Riffle area (ha)	Area of riffle habitat at each site (hectares)	0.03-0.16	0.05
	Pool area (ha)	Area of pool habitat at each site (hectares)	0.1-5.0	1.44

Table 2.2. Abundances of fish species collected along the Neosho and Cottonwood Rivers, KS June-August, 2013. Downstream/undammed data were collected downstream of low-head dam sites and at undammed sites (n = 10), while upstream data were collected upstream of low-head dam site (n = 5).

Common Name	Scientific Name	Abundance Downstream	Upstream	Total
Red Shiner	Cyprinella *lutrensis*	4,641	0	4641
Sand Shiner	Notropis *stramineus*	722	0	722
Bullhead Minnow	Pimephales *vigiliax*	523	0	523
Mimic Shiner	N. *volucellus*	387	105	492
Orangespotted Sunfish	Lepomis *humilis*	271	104	375
Slenderhead Darter	Percina *phoxocephala*	289	0	289
Central Stoneroller	Campostoma *anomalum*	265	0	265
Suckermouth Minnow	Phenacobius *mirabilis*	204	0	204
Bluntnose Minnow	P. *notatus*	128	0	128
Fantail Darter	Etheostoma *flabellare*	109	0	109
Bluntface Shiner	C. *camura*	66	0	66
Longear Sunfish	L. *megalotis*	44	1	45
Channel Catfish	Ictalurus *punctatus*	20	14	34
Ghost Shiner	N. *buchanani*	22	1	23
Logperch	P. *caprodes*	15	0	15
Freshwater Drum	Aplodinotus *grunniens*	0	12	12
Orangethroat Darter	E. *spectabile*	11	0	11
Carmine Shiner	N. *percobromus*	10	0	10
Fathead Minnow	P. *promelas*	8	0	8
White Crappie	Pomoxis *annularis*	5	3	8
Slim Minnow	P. *tenellus*	8	0	8
Brook Silverside	Labidesthes *sicculus*	6	0	6
Gizzard Shad	Dorosoma *cepedianum*	4	2	6
Freckled Madtom	Noturus *nocturnus*	5	0	5
Redfin Shiner	Lythrurus *umbratilis*	4	0	4
Golden Redhorse	Moxostoma *erythrurum*	4	0	4

Neosho Madtom	N. *placidus*	4	0	4
Largemouth Bass	Micropterus *salmoides*	3	0	3
Flathead Catfish	Pylodictis *olivaris*	3	0	3
Channel Darter	P. *copelandi*	3	0	3
Spotted Bass	M. *punctulatus*	2	0	2
Bluegill Sunfish	L. *macrochirus*	1	0	1
Green Sunfish	L. *cyanellus*	1	0	1
Smallmouth Bass	M. *dolomieu*	1	0	1
Slender Madtom	N. *exilis*	1	0	1
Stonecat	N. *flavus*	1	0	1

Chapter 3 - What and where can matter: habitat configuration within stream mosaics extends fish ecology and conservation to the riverscape

Abstract

Understanding the complex relationship between fish biodiversity and physical habitat is a precursor for effective aquatic conservation that is especially challenging for larger geographic scales (e.g., watershed, drainage, riverscape). Traditional approaches to understanding fish-habitat relationships that examine the role of individual physical conditions and isolated habitats have provided useful insights. However, additional approaches are needed to advance riverscape conservation in the face of accelerating environmental change. Landscape ecology has developed tools to look at a variety of patterns of spatial heterogeneity, but the transfer of useful landscape metrics to aquatic systems is still limited. We address this gap by quantifying habitat heterogeneity within and across stream mosaics that result from a combination of type (compositional heterogeneity), size, arrangement, and amount of configurational heterogeneity. We sampled fish biodiversity and aquatic habitat along ten 3-km sites within the Upper Neosho River sub-drainage, KS, from June-August 2013. Our research provided five take-home messages that can help researchers and managers understand riverscape habitat-fish biodiversity patterns. First, a survey that maps the spatial pattern of adjacent habitat patches within mosaics can be used to test the role of a range of compositional and configurational metrics. Specifically, we found stream habitats (pool, riffle, run, and glide) constituted discrete patches based upon stream width, depth, and flow velocity that formed varying mosaics of habitat across the riverscape. Second, variation within habitat types can affect biodiversity. For example,

considering all locations within the Neosho River, shallower, slower riffles had higher fish diversity. Third, select configurational heterogeneity metrics, particularly riffle and glide patch density, were useful predictors of stream fish biodiversity. More fish species were found in sites with higher riffle and glide patch density. Fourth, adjacent habitats can modify target habitat conditions and biodiversity. Thus, neighbors add additional heterogeneity to the whole-dataset generalizations. Finally, these metrics need to be linked to function to provide useful ecological and conservation insights. Because the relationship between spatial heterogeneity and biodiversity is critical for effective conservation of lotic ecosystems, many of the heterogeneity metrics we test here can start to extend fish ecology and conservation to the 'scape.

Introduction

Understanding the complex relationship between fish and physical habitat is a precursor for effective conservation of aquatic ecosystems. Addressing this organism-environment relationship at larger geographic scales (e.g., watershed, drainage, riverscapes) is critically important and especially challenging. Spatial habitat heterogeneity is ascribed to a landscape and refers to the uneven distribution of habitats of various sizes, shapes, and arrangements within an area. Heterogeneity influences ecological systems (e.g. Pervovic et al. 2015, Neumann et al. 2016) and effective conservation (Bunn and Arthington 2002, Palmer et al. 2010, Hovick et al. 2015). The roles of habitat type (Schlosser 1982, Vadas and Orth 2000; Fig. 3.1a) and amount (Magoulick 2000, Isaak et al. 2007, Fahrig 2013; Fig. 3.1b) are frequently examined. For example, stream fish communities associate with specific types of common habitats (e.g. pools and riffles) (Taylor 2000, Schwartz and Herricks 2008, Pegg et al. 2014), and the size (i.e., amount) of spawning habitat predicts Chinook salmon (*Oncorhynchus tshawytscha*) occurrence

(Isaak et al. 2007). In contrast, how habitats are arranged (Fig. 3.1c-d) is rarely examined in aquatic ecosystems (Palmer et al. 2000) even though configurational heterogeneity (i.e., the spatial arrangement of habitat patches) is central to the discipline of landscape ecology (Fahrig and Nuttle 2005, Cushman et al. 2008, Fahrig et al. 2011). Landscape ecology metrics have not been widely applied to aquatic systems even though quantifying the effect of different types of heterogeneity is the foundation of landscape ecology, possibly because existing metrics have not been clearly linked to system-specific function. Here, we examine the relationships between fish biodiversity and habitat metrics that quantify composition (what) and configuration (where) (Fig. 3.1a-d).

Traditional approaches that examine the relationship between physical conditions and the distribution of stream fishes have provided useful insights. First, fish assemblage composition and distribution have been associated with individual habitat variables such as depth (Schaefer 2001, Harvey and White 2017), flow velocity (Aadland 1993, Vadas and Orth 2001, Del Signore et al. 2016), habitat cover (Teresa et al. 2012, Lobon-Cervia et al. 2015) and substrate (Freedman et al. 2013, Zhoa et al. 2016). As examples, riffle-dwelling darter species can occur in deeper [Logperch (*Percina fulvitaenia*); Morris and Page 1981, Tiemann 2014] or shallower riffles [Orangethroat (*Etheostoma spectabile*) and Slenderhead (*P. phoxocephela*) darters; Cross 1967, Eberle 2014a, Edds 2014]. Ictalurid catfish species can associate with slower [Yellow (*Ameiurus natalis*) and Brown (*A. nebulosus*) bullhead; Pfleiger 1997] or faster habitats [Blue catfish (*Ictalurus furcatus*); Pflieger 1997]. Second, past studies of aquatic ecosystems have linked fish to specific habitat types (Taylor 200, Schwartz and Herricks 2008, Schwartz 2016). Common examples are specific fish associations with riffles, pools, and runs (Aadland 1993, Vadas and

Orth 2000, Persinger et al. 2011, Hitchman Chapter 1). This voluminous literature on habitat has provided a foundation for both research and conservation in aquatic systems.

Additional approaches to understanding fish-habitat relationships are needed to advance conservation in the face of accelerating environmental change in spite of this past progress on fish-habitat relationships. Globally, freshwater species are declining at high rates (Dudgeon et al., 2006; Vaughn, 2010), often because of alteration and degradation of the physical environment. A suite of anthropogenic disturbances such as agriculture (Piggott et al. 2015a, 2015b), urbanization (Chadwick et al. 2006, McDonald et al. 2014), land use change (Martinuzzi et al. 2013), and instream barriers (Pringle et al. 2000, Poff and Hart 2002) can degrade various components of physical habitat. As examples, agriculture (Chará-Serna et al. 2015) and urbanization (Knouft and Chu 2015) alter hydrology by reducing the quantity and quality of water, changing the magnitude and timing of flow peaks, and consequently altering depth, velocity, and substrate (Labbe and Fausch 2000, Lake 2003, Strauch et al. 2015). Land use and land use change affects local (e.g. water temperature, shoreline vegetation type; Olker et al. 2016). Low-head dams, like other instream barriers, affect sedimentation and local flow patterns (Stanley et al. 2002, Csiki and Rhoads, 2010, Fencl et al 2015), alter fish communities (Fencl et al. 2017) impede aquatic organism movements (Benstead et al. 1999), fragment the stream channel (Joy and Death 2001, Cumming 2004) and create other larger scale changes in physical habitat (Hitchman Chapter 2). Examining linked habitats, habitat-structure-function relationships, and 'scape patterns may help researchers and managers deal with these conservation challenges.

There is an emerging dichotomy that exists on whether to view landscapes as a collection of discrete habitat patches or as a continuum. The discrete patch model is central to landscape

ecology (Forman 1995, Turner et al. 2001). This model views landscape as a collection of discrete habitat patches. Alternative landscape models include the hierarchical patch dynamics model (Wu and Loucks 1995, Dunn and Majer 2007), the landscape variegation model (McIntyre and Barrett 1992, Costa et al. 2017), the island model (Shafer 1990) and continuous models (Austin 1985, Manning et al. 2004, Fischer and Lindenmayer 2006). The question, therefore, becomes when the discrete model is appropriate over alternative models including the continuous model. The approach to how habitat is defined in a study determines which landscape model is appropriate. The discrete patch model often considers landscapes to be binary with habitat patches providing resources necessary for an organism's persistence within a patch. However, the discrete model can also include mosaics of patches of varying habitat quality but still exhibiting clear boundaries (Dunn and Majer 2007, Lindenmayer et al. 2007). Here, the discrete patch model is used to view landscapes and to develop the mosaic. Many ecosystems have been viewed as a mosaic of habitats including terrestrial (Law and Dickman 1998, Williams and Kremen 2007, Villemy et al. 2015), marine (Bulleri and Benedetti-Cechi 2006, Gross et al. 2017) and freshwater ecosystems (Arletlaz et al. 2011, Kliendl et al. 2015). Stream fishes have been found to associate with habitats (e.g. pools and riffles; Taylor 2000, Schwartz and Herricks 2008, Pegg et al. 2014); therefore, viewing streams as a mosaic of habitats is logical. However, some argue for pluralism in landscape models where a range of models may be required to understand complex ecological systems (Lindenmayer et al. 2007). Thus, we included some aspects of the continuous model to examine how habitat characteristics within a discrete patch influenced biodiversity.

A mosaic of habitats units along the stream channel can create complex physical patterns to which compositional and configurational landscape metrics can be applied. Landscape

93

mosaics can be perceived as interconnected habitat patches that individually vary in structure and function and together create complex but predictable patterns of heterogeneity (Hitchman Chapter 1, Chapter 2). Stream habitat patches can result from distinct combinations of stream width, water depth, flow velocity, and substrate (Angermeier and Schlosser 1989) that create pools, riffles, glides, and runs (Rincón 1999, Hitchman Chapter 1, Chapter 2). Riffles are areas of high gradient with fast-flowing, turbulent water and coarser substrates; runs are areas with relatively fast-flowing water that are deeper than riffles with no turbulence. Glides are characterized by wide habitats with relatively low flow velocities and no turbulence; pools are the deepest waters of all four, with slower currents and finer sediments (Rincón 1999). These common habitat types can link aquatic community structure (Yeiser and Richter 2015, Cheek et al. 2016, Hitchman Chapter 1). Some fishes are exclusively recorded in runs or riffles, whereas others are typical inhabitants of pools (Schlosser 1982, Lobb & Orth 1991, Schwartz and Herricks 2008).

Landscape ecology can offer additional approaches to address spatial heterogeneity in natural systems (Turner et al. 2001, Fausch et al. 2002, Wiens 2002). In landscape ecology, heterogeneity is defined both as the type and diversity of habitats (compositional heterogeneity) and the size, shape, and arrangement habitats (configurational heterogeneity; Fahrig et al., 2015). Landscape ecology metrics have provided useful tools to examine the effects of both types of heterogeneity on terrestrial biodiversity. For example, compositional metrics for habitat type (Wagner et al. 2000, Weibull et al. 2003) and habitat diversity (Poulson 2002, Williams et al. 2002), as well as, configurational metrics for habitat size (Wagner and Edwards 2001, Kumar et al. 2006), shape (Helzer and Jelinski 1999, Moser et al. 2002) and connectivity (Ricketts 2001, Steffan-Dewater 2003) can influence species distributions and biodiversity. Some aquatic

researchers have applied landscape approaches to fish-habitat relationships (Schlosser 1995, Mossop et al. 2017). However, development of useful landscape metrics for aquatic systems, especially for configurational heterogeneity, is still limited (however, see Johnson and Gage 1997, Johnson and Host 2010). Thus, a gap exists in quantifying habitat heterogeneity within and across stream mosaics that result from a combination of type (compositional heterogeneity; Fig. 3.1-Q1a), size (Fig. 3.1-Q1b), arrangement (Fig. 3.1-Q1c), or amount of configurational heterogeneity (Fig. 3.1-Q1d).

Here we ask five specific research questions that examine how different patterns of heterogeneity affect fish biodiversity in riverscapes (Fig. 3.1). Before either compositional or configurational heterogeneity can exist, distinct habitat types must be arranged in a variety of spatial patterns. To evaluate this precursor to different types of heterogeneity, first, we tested if stream width, depth, and flow velocity clustered into discrete habitat types and if these habitat types were arranged in different combinations of habitat mosaics (Fig. 3.1-Q1). Second, variation in physical characteristics within discrete habitat types creates an additional type of compositional heterogeneity (Fig. 3.1-Q2). To quantify the effect of heterogeneity within a discrete habitat type, we examined how variation in depth and flow velocity within the discrete riffle habitat type influenced fish biodiversity. Because geographic location of habitats within the riverscape is an important component of heterogeneity, as an extension of this second question, we linked high-low velocity, shallow-deep riffles to spatial location (Fig. 3.1-Q3). Fourth, we asked if three common configurational heterogeneity metrics common in landscape ecology [e.g., patch size (area), patch shape (perimeter to area), patch density (number of riffle, run, pool, glide habitat patches within each mosaic)] influenced fish biodiversity (Fig. 3.1-Q4a, b, c). Many species have minimum area requirements (Wenny et al. 1993, Beier et al. 2002, Dardanelli et al.

2006), thus patch size in general (Munguia-Rosas and Montiel 2014) and specifically patch area (Lawton 2000, Scheiner et al. 2011) may increase species richness. Patch shape can affect the amount of habitat affected by edge effects, thus, patch shape, as measured by higher perimeter-area ratios, may increase stream fish biodiversity. Patch density is another configurational heterogeneity metric that can be positively associated with increased biodiversity metric (Rüdisser et al. 2015, Chambers et al. 2016, Fraga-Ramirez et al. 2017) through a variety of mechanisms. Finally, we asked how adjacent habitats (upstream or downstream) influence environmental variables and fish biodiversity (Fig. 3.1-Q5) because the influence of neighboring habitats is an important form of configurational heterogeneity (Glass and Floyd 2015, Ollivier et al. 2015). Throughout, we often prioritize the riffle because this keystone habitat can disproportionately affect biodiversity (Hitchman Chapter 1).

Materials and Methods

Study Area

Our study was conducted within the Upper Neosho River Basin along the upper Neosho River and lower Cottonwood River, two 5th order streams located KS, USA. The UNRB drains approximately 7,770 km2 upstream of the John Redmond Reservoir in Morris, Lyon, and Chase Counties, KS. Mean annual discharge at our sample sites was 8.72 m3/s (SE± 0.94, USGS gage 07179730, 1963-2013) for the Neosho River and 24.55 m3/s (SE± 2.19, USGS gage 07182250, 1963-2013) for the Cottonwood River.

In order to examine heterogeneity, we mapped adjacent habitat patches for 3 km at ten sites within the Upper Neosho River sub-drainage (Fig. 3.2). This project was undertaken in conjunction with a larger project that investigated potential impacts of low-head dams on the

96

native stream fish community. Although differences existed in scape-scale metrics at dams (Hitchman Chapter 2), no direct and consistent statistical differences in number of patches per habitat type existed between dammed and undammed sites (W = 17, p = 0.42; Wilcoxon rank sum test). Therefore, all sites were analyzed together.

General Sampling Regime

A continuous view of streams that encompasses mutli-scale spatial heterogeneity is essential for effective research and conservation within lotic ecosystems (Fausch et al. 2002). Patterns of environmental conditions in lotic ecosystems create a mosaic of habitats units along the stream channel. The approach used for this study (e.g. mosaic approach) quantified type and arrangement of habitat patches by employing a continuous survey to map stream habitat units. We continuously mapped habitat patches (pool, riffle, run, and glide) within each of ten 3 km sites to examine habitat mosaics. From June-August 2013, we identified, measured, and mapped the incidence and locations of habitat patches based on agreement by two independent observers using an objective series of stream channel morphology, surface flow, depth, and sediment composition (McCain et al. 1990, Harvey and Clifford 2009). Each sample location (N = 10) was considered a habitat mosaic. We quantified the spatial location of habitat patches by using trackplots at 5-s intervals and waypoints at the upper and lower boundary for each habitat unit from a handheld Garmin GPSmap76Cx (Garmin International, Olathe, KS). The mosaic approach is spatially explicit and allows for the quantification of the number, size, and arrangement of habitat units (pool, riffle, run, and glide) across the riverscape as well as distance between and among habitat patches. Sampling occurred during baseflow conditions (13.0-19.0 m3s-1; USGS gage 07182250). Trackplots and waypoints for each sample site were imported

into ArcMap v. 10.2 (ESRI, Redlands, CA). Habitat patches at each site were digitized into polygons and converted to raster format.

Habitat Patch Characteristics

Environmental variables (i.e., wetted stream width, water depth, and flow velocity) were measured within up to five patches of each habitat type (pool, riffle, run, and glide) at each of ten 3-km sites. At sites with less than five habitat patches of a habitat type, then all patches were sampled (at minimum = 3). All patches of a particular habitat type were sample at sites that contained < 5 of a particular habitat type. These channel units are described in detail in Chapter 1. Wetted stream width was recorded using a Nikon 8398 range finder (<1 m accuracy, range 3-200 m) at the midpoint of each habitat patch. Cross-stream transects of five equally-spaced points were used to collect depth and water velocity measurements. Flow velocity (60% of the depth) was measured with a Marsh-McBirney (Loveland, CO) Model 2000 flowmeter.

Fish-Biodiversity Sampling

We captured fish using a two- person mini-Missouri trawl to quantify fish biodiversity. The mini-Missouri trawl has been used to capture both small and large-bodied benthic fish (e.g., Herzog et al. 2009, Driver and Adams 2013, Starks et al. 2015). We chose the mini-Missouri trawl to ensure consistent sampling across habitats and study sites as it can be used in wadeable and non-wadeable areas. Two people pulled the trawl through a standard 30 m transect from upstream to downstream within each habitat sampled. More details on the mini-Missouri trawl and fish sampling appear in Chapter 1. Fish were returned alive to the stream after enumerated and identified to species.

Data Analysis

Question 1: Are habitat patches discrete and does the arrangement of patches differ across riverscape mosaics?

We used non-metric multidimensional scaling (NMDS) to evaluate if the habitat patch types (riffles, runs, pools, glides) were distinct and discrete (i.e., not continuous) based on the environmental variables (stream width, water depth, and flow velocity). NMDS has been shown to be a robust technique for analyzing ecological data (Minchin 1987). Environmental variables were log-transformed to satisfy statistical assumptions. For the NMDS, we used a Bray-Curtis distance matrix that quantified the similarity among patches for which habitat type was the factor (row) and environmental variables were the response variable (column) within the metaMDS function (distance = bray) in the R package vegan (Oksanen et al. 2013). Each habitat sample was plotted (N = 142). We then plotted 95% confidence ellipses for the mean (group centroids) by calculating standard error, which gives information about the sampling distribution of the mean centroid (as opposed to calculating based upon standard deviation, which is a measure of the spread of the data). Separation for each habitat type was analyzed using analysis of similarity (ANOSIM) in which a *p* value < 0.05 indicated a discrete, distinct, and unique habitat type based upon the environmental variables. If physical variables cluster in discrete categories, then the potential for mosaics of distinct habitat patches exists.

We used a series of longitudinal profile plots to illustrate variation in the diversity, sequence, and size of habitat patches within and across each potential 3-km mosaic. To create each longitudinal profile plot, the length (meters) of each habitat type patch was plotted from upstream to downstream (X axis). Habitat type was identified by color. The area of each patch

(hectares) was quantified on the Y axis. Plots were created using the R package ggplot2 (Wickam 2009). Habitat length and area were calculated from raster files for each site using ArcMap v. 10.2 (ESRI, Redlands, CA). In addition to the profile plots, we calculated the number of patches and overall habitat heterogeneity (Shannon's Diversity Index) for each site. We then used chi square to test if habitat mosaics varied significantly across sample sites. If profiles are composed of different combinations of patches (different colored patches in different combinations), then different patterns of configurational heterogeneity exist.

Question 2: Do habitat characteristics within riffle habitat influence fish biodiversity?

To investigate if specific riffle characteristics were linked to species richness, we ran linear regression models to examine relationships between species richness and environmental variables (width, depth, flow velocity) within discrete riffle patches.

Question 3: Where are the high biodiversity habitats located?

We plotted locations of high diversity riffles on the watershed map to see if there was a link between within riffle variation and geographic locations, i.e., all high in the watershed or low in the watershed.

Question 4: Which configurational metrics were related to biodiversity?

At each 3-km site, we calculated mean patch size (size), patch perimeter-area ratio (shape), and patch density using an ArcGIS planform map that was converted from a polygon-based feature file to a raster format and inputted into FRAGSTATS 4.1 (McGarigal et al. 2012). All metrics were calculated for each habitat type (pool, riffle, run, and glide). We then combined

multiple regression and an inference-theoretic approach [Akaike information criterion modified for small sample size (AIC_c) (Burnham and Anderson 2002)] to identify the best-approximating model for species richness as it relates to the predictor variables. To reduce the number of models, we examined pairwise correlations among each predictor variable (Table C.1). When a pair of predictors were highly correlated (> 0.70), the predictor that correlated highest with other variables was dropped from the analysis. Next, predictors were omitted from models if they had a variance inflation factor >10 or condition index >30. For parsimony, we limited each candidate model to one (N = 9) or two predictor variables (N = 36). Predictors were then standardized by subtracting the mean and dividing by the standard deviation. Models with the lowest AIC_c and the highest Akaike weights were considered the top candidate models. Only models with ΔAIC_c scores < 2 were interpreted (Burnham and Anderson 2002). Models were run using the *MuMin* package under the R platform (R Development Core Team 2013).

The simplest measure of configuration is patch size, which represents a fundamental attribute of the spatial character of a habitat patch. Mean patch size is a function of the number of patches for a particular habitat type (e.g. riffles) and total area encompassed by that habitat type. Perimeter-area ratio is a simple measure of shape complexity. Perimeter-area ratio is the ratio of patch perimeter to area in which patch shape is linked to patch size. Patch density is considered an important structural component of patch mosaics and can be used to facilitate comparisons of habitats and landscapes of different sizes. Patch density equals the total number of patches per 100 hectares for each habitat type (class level) or at each sample site (landscape level).

Question 5: Do adjacent habitats influence habitat-specific characteristics and biodiversity?

Multivariate analysis of variance (MANOVA) was used to examine the influence of adjacent habitats on environmental variables (stream width, depth, and flow velocity) within a target habitat. For example, we investigated how environmental variables within pool habitat (target) would change when a riffles was present (adjacent habitat) both upstream and downstream. The analysis was performed for each target habitat (pool, riffle, run, and glide) and all combinations of adjacent habitat both upstream and downstream (N = 24). All statistical analyses were performed using R software (R Development Core Team 2013). Although we ran all combinations of target and neighbor habitats for the MANOVA, we only present significant relationships.

Next, we used structural equation modeling (path analysis) to examine the effects of adjacent habitats on the environmental variables within a target habitat and how that relationship influenced fish species richness. Path analysis is based upon the calculation of path coefficients (standardized partial regression coefficients), which can be used to calculate direct and indirect effects (Grace 2006). Direct effects are the path coefficients between two variables connected by a path. Indirect effects are effects mediated through another variable (e.g. habitat). We chose path analysis because it can simultaneously evaluate direct and indirect effects of neighboring habitats on species richness. The analysis was performed for all combinations of target habitats (pool, riffle, run, and glide) and adjacent habitat both upstream and downstream. Standardized path coefficients (standardized β) indicated the strength of relationships and R^2 quantified the amount of variation explained by specific sets of variables. We used the library lavaan with function sem in R (Rosseel 2012). Analyses were performed using the R platform (R

Development Core Team 2013). Although we ran all combinations of target and neighbor habitats for path analysis, we only present significant relationships.

Results

Question 1: Are habitat patches discrete and does the arrangement of patches differ across riverscape mosaics?

Riffle, run, pool, and glide habitat categories were quantitatively distinct. We plotted 95% confidence ellipses for the mean (group centroid) for each habitat type. Lack of overlap among the ellipses indicates pools, riffles, runs, and glides act as discrete habitat units based upon stream width, depth, and flow velocity). Specifically, glide, pool, riffle, and run habitats differed in width, depth, and flow velocity (ANOSIM Global R = 0.30, p < 0.001; Fig. 3.3). Riffles and runs were characterized as fast-flowing habitats with runs deeper than riffles (Fig. 3.3). Pools were the slowest and deepest habitats (Fig. 3.3). Glides were also slow-flowing habitats and shallower than pool (Fig. 3.3).

Mosaics differed in the type and sequence of habitat patches across all ten 3-km sample sites (Fig. 3.4). For example, Sites 1 and 2 were characterized as having a high number of patches and high habitat diversity (Fig. 3.4a, b). Site 7 was characterized as having a fewer number of patches and the lowest habitat diversity (Fig. 3.4g). Pool, riffle, and run habitats were present across all sites. Glides were irregularly distributed and were most commonly associated with riffles and pools (adjacent to pools 68-74%; adjacent to riffles 19-21%). The number and type of habitat patches varied across study sites ($\chi2 = 70.42$, *p* < 0.001; Fig. 3.4). The total number of patches per 3-km ranged from 17 (Fig. 3.4j, Site 10) to 59 (Fig. 3.4b, Site 2). Overall habitat diversity ranged from 0.56 (Fig. 3.4g, Site 7)-1.15 (Fig. 3.4a, b, Site 1, 2).

Question 2: Do habitat characteristics within riffle habitat influence fish biodiversity?

Habitat-specific fish sampling occurred within 143 unique habitat patches. We sampled a total of 7,791 fish representing 35 species across seven families at ten sites within the Upper Neosho River sub-drainage (Table A.1).

Although riffles were distinct from other habitat types, slow, shallow riffles had more fish species. Species richness was inversely related to riffle depth ($R^2 = 0.37$; $p = 0.001$, Fig. 3.5a). Species richness was highest within shallow riffles (Fig. 3.5a). Species richness was highest within low velocity riffles ($R^2 = 0.25$; $p = 0.02$, Fig. 3.5b). Combined, species richness was greatest within shallow, slow flowing riffles (Fig. 3.5a, b). No significant relationship existed between species richness and riffle width ($R^2 < 0.01$; $p = 0.64$).

Question 3: Where are the high biodiversity habitats located?

Species richness was highest within shallow riffles located at sample sites 1, 2, and 7 (Fig. 3.5c). Species richness was highest within low velocity riffles at sites 1, 2, 4, 7, and 8 (Fig. 3.5d). Combined, species richness was greatest within shallow, slow flow riffle habitat at sample sites 1, 2, and 7 (Fig. 3.5c, d).

Question 4: Which configurational metrics were related to biodiversity?

Select configurational heterogeneity metrics, common in landscape ecology, were related to increased species richness. We examined three configurational metrics (mean patch size, perimeter-area ratio, and patch density) for four habitat types (pool, riffle, run, and glide). We examined all pairwise correlations (N = 66; Table C.1). Metrics characterizing pool habitat were

correlated with one another (> 0.75; Table C.1). Glide patch density was correlated with glide perimeter-area ratio (> 0.75; Table C.1). Finally, riffle patch density was correlated with glide patch density (0.75; Table C.1). Out of a possible 45 models examined using multiple linear regression, only four models were included in the set of candidate models (ΔAIC_c scores < 2; Table 3.1). The top ranked model predicting fish species richness included riffle patch density and riffle area ($R^2 = 0.75$; $p = 0.004$; Table 3.1). The next best models included riffle patch density and glide area ($R^2 = 0.73$; $p = 0.004$; Table 3.1), riffle patch density and riffle perimeter-area ratio ($R^2 = 0.71$; $p = 0.005$; Table 3.1) and riffle patch density and run area ($R^2 = 0.69$; $p = 0.007$; Table 3.1). The most important variable explaining fish species richness was riffle patch density which explained 74% of the variation on average and was included in all models (variable importance = 1; Table 3.1).

Question 5: Do adjacent habitats influence habitat-specific characteristics and biodiversity?

For select combinations, neighboring patches altered environmental characteristics of target patches and, in some cases, species richness. Of the 24 target-neighbor habitat combinations tested, we observed six significant effects of neighbor on physical habitat attributes, of which three physical target-physical combinations were linked to significant changes in specific richness. First, flow velocity was higher in pool habitats (target) directly above runs ($F = 6.37$; $p < 0.01$; Fig. 3.6a). Second, run habitats (target) were moderately deeper when downstream of pools ($F = 3.07$; $p < 0.1$; Fig. 3.6b). Third, glide habitats (target) were significantly faster upstream of riffles ($F = 6.00$; $p < 0.01$; Fig. 3.6c). None of these physical changes resulted in changes to species richness. Fourth, stream depth was significantly shallower in riffle (target) habitats ($R^2 = 0.11$; $p < 0.05$; Fig. 3.7a) located immediately downstream of

glide habitats (F = 3.87; $p < 0.05$; Fig. 3.6d) which led to a significant increase in species richness ($R^2 = 0.26$; $p < 0.05$; Fig. 3.7a). Fifth, riffles were significantly deeper ($R^2 = 0.12$; $p < 0.05$; Fig. 3.7b) when downstream of run habitat (F = 3.87; $p < 0.05$; Fig. 3.6d), which led to a significant decrease in species richness ($R^2 = 0.31$; $p < 0.05$; Fig. 3.7b). Sixth, riffles were more shallow and narrow ($R^2 = 0.16$; $p < 0.05$; Fig. 3.7c) when upstream of glide habitats, increasing species richness ($R^2 = 0.26$; $p < 0.05$; Fig. 3.7c).

Discussion

Researchers and managers increasingly see a need to apply a landscape approach to aquatic systems (Wiens 2002, Allan 2004, Datry et al. 2016), but exactly how to operationalize this land to water transformation remains a challenge. Using both compositional and configurational habitat approaches can help address fish-habitat relationships across the riverscape. Research in aquatic ecosystems has indicated that both compositional (Yarnell et al. 2005, Schwartz and Herricks 2008) and configurational metrics (Palmer et al. 2000, Isaak et al. 2007) influence aquatic biodiversity. Our research provides five take-home messages that researchers and managers can apply to understanding biodiversity riverscape habitat-fish biodiversity patterns. First, a survey that maps the spatial pattern of adjacent habitat patches within mosaics can be used to test the role compositional and configurational metrics. Second, within habitat characteristics are important predictors of within habitat biodiversity. Third, some configurational heterogeneity metrics, particularly riffle patch density, are useful predictors of stream fish biodiversity. Fourth, adjacent habitats can influence neighboring habitat characteristics and biodiversity. Finally, these metrics need to be linked to function to provide useful ecological and conservation insights.

The mosaic approach illustrated riverscape patterns of habitat and fish biodiversity and facilitated tests of an array of spatial heterogeneity relationships. Our research showed that stream habitats (pool, riffle, run, and glide) were functionally distinct units characterized by stream width, water depth, flow velocity. These discrete and distinct habitat patches created connected aquatic mosaics along the stream channel. The majority of fish habitat studies have considered these habitats as separate, isolated units (Schlosser 1982). However, our maps of connected habitats allowed for the quantification of various configurational heterogeneity metrics that can then be used to go beyond simply linking stream fishes to a particular individual habitat and facilitate a more in-depth investigation about how those habitat arrangements across the riverscape influences stream fish. Additionally, in large sand bed rivers like the Kansas or Smoky Hill, habitat diversity (type and arrangement) maybe so low as to make examining composition and configuration of these habitats types unimportant. For these systems, another approach to quantifying the role of spatial heterogeneity is needed. Whereas, in many other streams, habitat types are likely distinct, diverse, and variable. Thus, an advantage of the mosaic approach is that this approach reveals patterns to which compositional and configurational metrics can be applied in order to detect underlying ecological patterns for both common and uncommon habitat patches. Though the mosaic approach has linked habitat to aquatic community structure (Yeiser and Richter 2015, Cheek et al. 2016), it is not commonly applied to aquatic ecosystems. Because mosaics are rarely mapped, we don't at present know how the results from the Upper Neosho River Basin relate to other stream systems. Our research suggests that this mosaic approach should be more widely applied to aquatic ecosystems because viewing streams as a connected habitat mosaic may improve the chances of elucidating the effects of landscape configuration on biodiversity.

Some configurational metrics were functionally important. Riffle patch density was the most important predictor for stream fish biodiversity. Patch density has been found to be functionally important in terrestrial studies (Wasserman et al. 2012, Shirk et al. 2014, Cushman et al. 2013). For example, lizard diversity was positively associated with patch density of tropical dry desert (Fraga-Ramirez et al. 2017). Here, high patch density of riffles could be associated with a higher number of functionally important habitat patches available to stream fishes (Tews et al. 2004). Riffles are small habitats that occurred across all study sites and are functionally important. Riffles have been described as keystone habitat for fishes in the Upper Neosho River Basin in that they disproportionately increase biodiversity relative to their proportion across the riverscape (Hitchman Chapter 1). Riffles may be of particular importance in this system. Riffles are spaced an average of five to seven channel widths in undisturbed streams (Leopold et al. 1964); however, due to the numerous low-head dams and a history of gravel mining, the system may become sediment starved making riffles a rarity (Kondolf 1997). Riffles serve as spawning and rearing habitat, foraging areas and provide refuge from predators (Schlosser 1987, Gillette 2012, Teichert et al. 2013), therefore, areas of high riffle density would provide important, functional habitats in the study area. Metrics characterizing the size and shape of habitats (e.g. riffle, glide run area) were also predictors of fish species richness. Mean patch size has been found to influence species richness in terrestrial systems (Robbins et al. 1989, Bender et al. 1998, Kumar et al. 2006) and may be linked to species-area relationships. However, riffle patch density explained most of the variation among all models and may have carried these other metrics. Many of the metrics we examined were not linked to species richness however. For example, none of the metrics for pools were related to species richness. Therefore, a general transfer of

landscape ecology metrics does not work all the time and careful thought needs to be put into identifying ecologically important metrics.

A key finding from our study indicated species richness was higher among shallow, slow-flowing riffles. Here, we examined how within habitat characteristics across all riffles in the study influenced species richness by taking a continuous view of landscapes. Shallow riffles are essential habitat for macroinvertebrates (fish prey items) and necessary for the completion of life histories for stream fishes (Aadland 1993, Brewer et al. 2006). Many species in the Neosho River Basin [e.g. orangethroat darter (*E. spectabile*), central stoneroller (*Campostoma anomalum*), and fantail darter (*E. flabellar*) associate with shallow riffles (Cross 1967, Eberle 2014b, Gillette 2014). Additionally, this relationship may correspond to preferred spawning habitats. For example, Brewer et al. (2006) found that many riffle-dwelling species move into shallow and/or slow flowing riffles to spawn. Shallow riffles provide refuge from predation of piscivorous fishes (Schlosser 1987, Winemiller and Jepsen 1998), which results in an increase in the number of species.

Adjacent habitats can influence neighboring habitat characteristics and biodiversity. Habitats generally took on characteristics of flow velocity and depth of neighboring habitats in our study. Flow velocity within pools and glides increased when adjacent to fast-flowing habitats (e.g. riffles and runs). Runs were deeper downstream of pool habitat (characterized as the deepest habitat in our study). Occasionally, adjacent habitats can alter biodiversity in neighboring habitats. For example, bird species richness was found to be higher in aspen woodlands adjacent to riparian habitat relative to aspen stands located farther away (Glass and Floyd 2015). In streams, channel darters (*Percina copelandi*) had a strong affinity for riffles upstream of run and pool habitat (Reid et al. 2005). Path analysis was a useful tool that allowed

us to identify indirect effects adjacent habitat had on species richness. Adjacent habitats in our study influenced fish species richness primarily through mediated habitat effects. Riffles were deeper when located downstream of run habitats, which led to a decrease in species richness. When riffles were adjacent to glide habitats (both upstream and downstream), riffles were shallower and species richness increased. These findings are consistent with the within habitat analysis where species richness was higher within shallow riffles even though one analysis (within habitat characteristics) collectively considered all riffles in the study, whereas the other (adjacent habitats) was habitat specific. In our analysis, position of neighbors could alter characteristics of target patches, which is a new and exciting insight. Position could also influence a range of other habitat metrics such as size or shape. These hypotheses can be tested in future studies within this and other systems. In summary, the above results indicate that spatial arrangement (e.g. placement of habitats) and characteristics of habitat does matter and pluralism of landscape models should be taken into account when developing conservation strategies for stream fishes.

To transfer landscape ecology approaches to lotic ecosystems, research questions should be focused and functionally matched to metrics. This study was not an exhaustive exploration into the best landscape metrics to be used in lotic ecosystems. Our research was intended to test if various metrics of configurational heterogeneity provided different information about a study system and thus should be considered in greater detail in the future. Landscape metrics are promising tools to measure aquatic biodiversity (Johnson and Host 2010). A variety of metrics have been suggested, however, many of them are complex and their ecological meaning is not always evident (Wiens 2002, McGarigal et al. 2012). Therefore, careful thought needs to be given to the number of metrics relative to sample sizes used in a study. Additionally, many

packages designed to calculate landscape metrics (e.g. FRAGSTATS, Spatial Analyst) have

lowered technological barriers, thus allowing users to calculate a variety of landscape metrics

without an understanding of how each metric relates functionally to ecological processes (Kupfer

2012). For example, metrics used to describe connectivity in terrestrial ecosystems may not be

applicable to lotic ecosystems due to their linear structure and unidirectional flow. Therefore, an

understanding of the link between study system and response (e.g. energy flow, biodiversity,

movement, etc.) needs to be thoughtfully considered when identifying which landscape metrics

to use in a study. A conceptual framework that outlines possible metrics and approaches to

describing spatial heterogeneity (Fig. 1) can be a useful strategy for taking landscape ecology

approaches to aquatic ecosystems.

Understanding the influence various measures of configurational heterogeneity have on

biodiversity can aid in the conservation of stream fishes. We identified riffle patch density as a

significant predictor of fish species richness. Riffles are important habitats for maintaining fish

biodiversity (Hitchman Chapter 1). If management goals are to conserve overall native

biodiversity, then increasing the density of riffles and/or glides may be important. However,

patch density alone should not be the only consideration for effective conservation strategies.

Riffles were positively impacted when located upstream and downstream of glide habitats and

downstream of run habitats. Thus, consideration should also be given to how the habitats are

arranged along the mosaic. Additionally, the spatial location of high biodiversity habitats (e.g.

riffles) is useful for identifying target conservation areas for habitat specialist species. For

example, the threatened Neosho madtom (*Natorus placidus*), whose distribution is currently

declining due to habitat destruction and fragmentation, is a riffle-dwelling species primarily

distributed along the Neosho and Cottonwood Rivers. Neosho madtom prefer shallow riffles

with loose substrate (Moss 1981, Wildhaber 2014). Diverse species in our study area preferred shallow, low-velocity riffles concentrated at sites 1, 2, and 7. However, since site 1 and 2 are above the distribution of the Neosho madtom, conservation efforts for mitigating riffles and gravel bars should concentrate around site 7. Our research illustrates how multiple measures of compositional and configurational heterogeneity can be used for the conservation of stream fishes.

The mosaic approach allows for a holistic view of riverscapes. Emerging techniques exist to incorporate high-resolution, spatially explicit data to understand pattern and process at the riverscape scale (Carbonneau et al. 2012). The approach can incorporate multiple landscape models to quantify multiple measures of heterogeneity both within (continuous) and across (discrete) habitats. Additionally, the mosaic approach can extend to other theoretical concepts in ecology that include island biogeography, source-sink dynamics, and metacommunities. For example, scientists and managers can use the mosaic approach to identify high-quality patches along a mosaic of patches that serve as sources to other, low-quality habitats. Our use of mosaics in examining heterogeneity in this chapter and in testing other ideas in associated research (Chapter 1, Chapter 2) have led to new ways to conceptualize stream communities (e.g., mosaic approach, keystone habitats, mediated dam effects). The generality of these insights to other individual stream systems and other stream types needs to be tested. However, our research sets up clear testable hypotheses that have relevance to ecological research, conservation, and restoration.

References

Aadland LP (1993) Stream habitat types: their fish assemblages and relationship to flow. North American Journal of Fisheries Management, **13**, 790–806.

Allan JD (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems. Annual Review of Ecology Evolution and Systematics, **35**, 257-284.

Angermeier PL, Schlosser IJ (1989) Species-area relationships for stream fishes. Ecology, **70**, 1450-1462.

Arlettaz R, Ligon A, Sierro A, Werner P, Kery M, Oggier PA (2011) River bed restoration boosts habitat mosaics and the demography of two rare non-aquatic vertebrates. Biological Conservation, **144**, 2126-2132.

Austin MP (1985) Continuum concept, ordination methods, and niche theory. Annual Review of Ecology and Systematics, **16**, 39-61.

Beier P, Van Drielen M, Kankam BO (2002) Avifaunal collapse in West African forest fragments. Conservation Biology, **16**, 1097-1111.

Benstead JP, March JG, Pringle CM, Scatena FN (1999) Effects of a low-head dam and water abstraction on migratory tropical stream biota. Ecological Applications, **9**, 656-668.

Brewer SK, Papoulias DM, Rabeni CF (2006) Spawning habitat associations and selection by fishes in a flow-regulated prairie river. Transactions of the American Fisheries Society, **135**, 763-778.

Bulleri F, Benedetti-Cecchi L (2006) Mechanisms of recovery and resilience of different components of mosaics of habitats on shallow rocky reefs. Oecologia, **149**, 482-492.

Bunn SE, Arthington AH (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management, **30**, 492-507.

Camana M, Dala-Corte RB, Becker FG (2016) Relation between species richness and stream
slope in riffle fish assemblages is dependent on spatial scale. Environmental Biology of
Fishes, **99**, 603-612.

Carbonneau P, Fonstad MA, Marcus WA, Dugdale SJ (2012) Making riverscapes real.
Geomorphology, **137**, 74-86.

Chadwick MA, Dobberfuhl DR, Benke AC, Huryn AD, Suberkropp K, Thiele JE (2006)
Urbanization affects stream ecosystem function by altering hydrology, chemistry, and
biotic richness. Ecological Applications, **16**, 1796-1807.

Chambers CL, Cushman SA, Medina-Fitoria A, Martinez-Fonseca J, Chavez-Velasquez M
(2016) Influences of scale on bat habitat relationships in a forested landscape in
Nicaragua. Landscape Ecology, **31**, 1299-1318.

Chara-Serna AM, Chara J, Giraldo LP, Zuniga MD, Allan JD (2015) Understanding the impacts
of agriculture on Andean stream ecosystems of Colombia: a causal analysis using aquatic
macroinvertebrates as indicators of biological integrity. Freshwater Science, **34**, 727-740.

Cheek BD, Grabowski TB, Bean PT, Groeschel JR, Magnelia SJ (2016) Evaluating habitat
associations of a fish assemblage at multiple spatial scales in a minimally disturbed
stream using low-cost remote sensing. Aquatic Conservation-Marine and Freshwater
Ecosystems, **26**, 20-34.

Costa C, Oliveira VHF, Maciel R, Beiroz W, Korasaki V, Louzada J (2017) Variegated tropical
landscapes conserve diverse dung beetle communities. Peerj, **5**.

Cross FB (1967) Handbook of fishes of Kansas. University of Kansas, Natural History Museum.

Csiki S, Rhoads BL (2010) Hydraulic and geomorphological effects of run-of-river dams.
Progress in Physical Geography, **34**, 755-780.

Cumming GS (2004) The impact of low-head dams on fish species richness in Wisconsin, USA. Ecological Applications, **14**, 1495-1506.

Cushman SA, McGarigal K, Neel MC (2008) Parsimony in landscape metrics: Strength, universality, and consistency. Ecological Indicators, **8**, 691-703.

Cushman SA, Shirk AJ, Landguth EL (2013) Landscape genetics and limiting factors. Conservation Genetics, **14**, 263-274.

Dardanelli S, Nores ML, Nores M (2006) Minimum area requirements of breeding birds in fragmented woodland of Central Argentina. Diversity and Distributions, **12**, 687-693.

Datry T, Pella H, Leigh C, Bonada N, Hugueny B (2016) A landscape approach to advance intermittent river ecology. Freshwater Biology, **61**, 1200-1213.

Del Signore A, Lenders HJR, Hendriks AJ, Vonk JA, Mulder C, Leuven R (2016) Size-Mediated Effects of Water-Flow Velocity on Riverine Fish Species. River Research and Applications, **32**, 390-398.

Driver LJ, Adams GL (2013) Life History and Spawning Behavior of the Western Sand Darter (*Ammocrypta clara*) in Northeast Arkansas. American Midland Naturalist, **170**, 199-212.

Dudgeon D, Arthington AH, Gessner MO *et al.* (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews, **81**, 163-182.

Dunn AG, Majer JD (2007) In response to the continuum model for fauna research: a hierarchical, patch-based model of spatial landscape patterns. Oikos, **116**, 1413-1418.

Eberle ME (2014a) Orangethroat darter, *Etheostoma spectabile* Agassiz 1854. Pages 410-412 *In* Kansas Fishes Committee. Kanas Fishes. University Press of Kansas, Lawrence, KS.

Eberle ME (2014b) Central stoneroller, *Campostoma anomalum* Rafinesque 1820. Pages 134-136 *In* Kansas Fishes Committee. Kanas Fishes. University Press of Kansas, Lawrence,

KS.

Edds DR (2014) Slenderhead darter, *Percina phoxocephala* Nelson 1876. Pages 428-429 *In* Kansas Fishes Committee. Kanas Fishes. University Press of Kansas, Lawrence, KS.

Fahrig L, Nuttle WK (2005) Population ecology in spatially heterogeneous environments. *In* Lovett GM, Jones CG, Turner MG, Weathers KC, eds. Ecosystem function in heterogenous landscapes, pp. 95–118. Springer, New-York.

Fahrig L, Baudry J, Brotons L *et al.* (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters*, **14**, 101-112.

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography*, **40**, 1649-1663.

Fahrig L, Girard J, Duro D *et al.* (2015) Farmlands with smaller crop fields have higher within-field biodiversity. Agriculture Ecosystems & Environment*, **200**, 219-234.

Fausch KD, Torgersen CE, Baxter CV, Li HW (2002) Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. Bioscience*, **52**, 483-498.

Fencl JS, Mather ME, Costigan KH, Daniels MD (2015) How big of an effect do small dams have? using geomorphological footprints to quantify spatial impact of low-head dams and identify patterns of across-dam variation. Plos One. 10, e0141210.doi:10.1371/journal.pone.0141210.

Fencl JS, Mather ME, Smith JM, Hitchman SM. (2017) The blind men meet the elephant at the dam: alternative spatial and taxonomic components reveal different insights about how low-head dams impact fish biodiversity. Ecosphere, 8 (11):e01973. 10.1002/ecs2.1973

Fischer J, Lindenmayer DB (2006) Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. Oikos*, **112**, 473-480.

Forman RTT (1995) Land mosaics: the ecology of landscapes and regions. Cambridge
University Press, Cambridge.

Fraga-Ramirez Y, Suazo-Ortuno I, Avila-Cabadilla LD, Alvarez-Anorve M, Alvarado-Diaz J
(2017) Multiscale analysis of factors influencing herpetofaunal assemblages in early
successional stages of a tropical dry forest in western Mexico. Biological Conservation*,*
209, 196-210.

Freedman JA, Stauffer JR, Stauffer JR (2013) Gravel dredging alters diversity and structure of
riverine fish assemblages. Freshwater Biology*,* **58**, 261-274.

Gillette DP (2012) Effects of Variation among Riffles on Prey Use and Feeding Selectivity of the
Orangethroat Darter Etheostoma spectabile. American Midland Naturalist*,* **168**, 184-201.

Gillette DP (2014) Fantail darter*, Etheostoma flabellare* Rafinesque 1819. Pages 400-401 *In*
Kansas Fishes Committee. Kanas Fishes. University Press of Kansas, Lawrence, KS.

Glass JR, Floyd CH (2015) Effects of proximity to riparian zones on avian species richness and
abundance in montane aspen woodlands. Journal of Field Ornithology*,* **86**, 252-265.

Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press,
New York.

Gross C, Donoghue C, Pruitt C, Trimble AC, Ruesink JL (2017) Taxonomic and functional
assessment of mesopredator diversity across an estuarine habitat mosaic. Ecosphere*,* **8**.
DOI: 10.1002/ecs2.1792

Harvey GL, Clifford NJ (2009) Microscale hydrodynamics and coherent flow structures in
rivers: Implications for the characterization of physical habitat. River Research and
Applications*,* **25**, 160-180.

Harvey BC, White JL (2017) Axes of fear for stream fish: water depth and distance to cover.

Environmental Biology of Fishes, **100**, 565-573.

Helzer CJ, Jelinski DE (1999) The relative importance of patch area and perimeter-area ratio to grassland breeding birds. Ecological Applications, **9**, 1448-1458.

Herzog DP, Ostendorf DE, Hrabik RA, Barko VA (2009) The Mini-Missouri Trawl: A Useful Methodology for Sampling Small-Bodied Fishes in Small and Large River Systems. Journal of Freshwater Ecology, **24**, 103-108.

Hovick TJ, Elmore RD, Fuhlendorf SD, Engle DM, Hamilton RG (2015) Spatial heterogeneity increases diversity and stability in grassland bird communities. Ecological Applications. **25**, 662-672.

Isaak DJ, Thurow RF, Rieman BE, Dunham JB (2007) Chinook salmon use of spawning patches: Relative roles of habitat quality, size, and connectivity. Ecological Applications, **17**, 352-364.

Johnson LB, Gage SH (1997) Landscape approaches to the analysis of aquatic ecosystems. Freshwater Biology, **37**, 113-132.

Johnson LB, Host GE (2010) Recent developments in landscape approaches for the study of aquatic ecosystems. Journal of the North American Benthological Society, **29**, 41-66.

Joy MK, Death RG (2001) Control of freshwater fish and crayfish community structure in Taranaki, New Zealand: dams, diadromy or habitat structure? Freshwater Biology, **46**, 417-429.

Kleindl WJ, Rains MC, Marshall LA, Hauer FR (2015) Fire and flood expand the floodplain shifting habitat mosaic concept. Freshwater Science, **34**, 1366-1382.

Kondolf GM (1997) Hungry water: Effects of dams and gravel mining on river channels. Environmental Management, **21**, 533-551.

Knighton D (1998) Fluvial forms and processes: A new perspective. Arnold, London.

Knouft JH, Chu ML (2015) Using watershed-scale hydrological models to predict the impacts of increasing urbanization on freshwater fish assemblages. Ecohydrology, **8**, 273-285.

Kumar S, Stohlgren TJ, Chong GW (2006) Spatial heterogeneity influences native and nonnative plant species richness. Ecology, **87**, 3186-3199.

Kupfer JA (2012) Landscape ecology and biogeography: Rethinking landscape metrics in a post-FRAGSTATS landscape. Progress in Physical Geography, **36**, 400-420.

Labbe TR, Fausch KD (2000) Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications, **10**, 1774-1791.

Lake PS (2003) Ecological effects of perturbation by drought in flowing waters. Freshwater Biology, **48**, 1161-1172.

Law BS, Dickman CR (1998) The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. Biodiversity and Conservation, **7**, 323-333.

Lawton JH (2000) Community Ecology in a Changing World. Ecology Institute, Oldendorf, Germany.

Leopold LB, Wolman MG, Miller JP. 1964. Fluvial Processes in Geomorphology. 522pp. Freeman, San Francisco.

Lindenmayer DB, Fischer J, Hobbs R (2007) The need for pluralism in landscape models: a reply to Dunn and Majer. Oikos, **116**, 1419-1421.

Lobb MD, Orth DJ (1991) Habitat use by an assemblage of fish in a large warmwater stream. Transactions of the American Fisheries Society, **120**, 65-78.

Lobon-Cervia J, Hess LL, Melack JM, Araujo-Lima C (2015) The importance of forest cover for

fish richness and abundance on the Amazon floodplain. Hydrobiologia, **750**, 245-255.

Magoulick DD (2000). Spatial and temporal variation in fish assemblages of drying stream
pools: The role of abiotic and biotic factors. Aquatic Ecology, **34**, 29-41.

Manning AD, Lindenmayer DB, Barry SC (2004) The conservation implications of bird
reproduction in the agricultural "matrix": a case study of the vulnerable superb parrot of
south-eastern Australia. Biological Conservation, **120**, 363-374.

Martinuzzi S, Radeloff VC, Higgins JV, Helmers DP, Plantinga AJ, Lewis DJ (2013) Key areas
for conserving United States' biodiversity likely threatened by future land use change.
Ecosphere, **4**, 1-13.

McCain M, Fuller D, Decker L, Overton K (1990) Stream habitat classification and inventory
procedures for northern California. FHC Currents. No.1. U.S. Department of Agriculture.
Forest Service, Pacific Southwest Region.

McDonald RI, Weber K, Padowski J *et al.* (2014) Water on an urban planet: Urbanization and
the reach of urban water infrastructure. Global Environmental Change-Human and Policy
Dimensions, **27**, 96-105.

McGarigal K, Cushman S, Ene E (2012) FRAGSTATS V4: Spatial pattern analysis program for
categorical and continuous maps, computer software program produced by the authors at
the University of Massachusetts, Amherst.
http://www.umass.edu/landeco/research/fragstats/fragstats.html

McIntyre S, Barrett GW (1992) Habitat variegation, an alternative to fragmentation.
Conservation Biology, **6**, 146-147.

Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological
ordination. Vegetatio, **69**, 89-107.

Morris MA, Page LM (1981) Variation in western logperches (Pisces: Percidae), with a description of a new subspecies from the Ozarks. Copeia, 95-108.

Moser D, Zechmeister HG, Plutzar C, Sauberer N, Wrbka T, Grabherr G (2002) Landscape patch shape complexity as an effective measure for plant species richness in rural landscapes. Landscape Ecology, **17**, 657-669.

Moss RE (1981) Life history information for the Neosho madtom (Natorus placidus). Kansas Department of Wildlife and Parks, Final Report, Pratt, KS.

Mossop KD, Moran NP, Chapple DG, Wong BBM (2017) Connectivity and habitat type shape divergent dispersal behavior in a desert-dwelling fish. Landscape Ecology, **32**, 1065-1078.

Munguia-Rosas MA, Montiel S (2014) Patch Size and Isolation Predict Plant Species Density in a Naturally Fragmented Forest. Plos One, **9**.

Neumann JL, Griffiths GH, Hoodless A, Holloway GJ (2016) The compositional and configurational heterogeneity of matrix habitats shape woodland carabid communities in wooded-agricultural landscapes. Landscape Ecology, **31**, 301-315.

Oksanen J, Blanchet FG, Kindt R *et al.* (2013) Vegan: Community ecology package. R package version 2.0-9. http://CRAN.R-project.org/package=vegan.

Olker JH, Kovalenko KE, Ciborowski JJH, Brady VJ, Johnson LB (2016) Watershed Land Use and Local Habitat: Implications for Habitat Assessment. Wetlands, **36**, 311-321.

Ollivier QR, Bramwell NA, Hammill E, Foster-Thorpe C, Booth DJ (2015) Are the effects of adjacent habitat type on seagrass gastropod communities being masked by previous focus on habitat dyads? Australian Journal of Zoology, **63**, 357-363.

Palmer MA, Swan CM, Nelson K, Silver P, Alvestad R (2000) Streambed landscapes: evidence

that stream invertebrates respond to the type and spatial arrangement of patches. Landscape Ecology, **15**, 563-576.

Pegg MA, Behmer AT, Parasaweicz P, Rogers JN (2014) Application of mesohabitat fish use information to identify guilds for lotic systems. Journal of Applied Ichthyology, **30**, 1065-1068.

Perovic D, Gamez-Virues S, Borschig C *et al.* (2015) Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. Journal of Applied Ecology, **52**, 505-513.

Persinger JW, Orth DJ, Averettz AW (2011) Using habitat guilds to develop habitat suitability criteria for a warmwater stream fish assemblage. River Research and Applications, **27**, 956-966.

Peterson JT, Rabeni CF (2001) Evaluating the physical characteristics of channel units in an Ozark stream. Transactions of the American Fisheries Society, **130**, 898-910.

Pflieger WL (1997) The Fishes of Missouri, revised edition. Missouri Department of Conservation, Jefferson City.

Piggott JJ, Salis RK, Lear G, Townsend CR, Matthaei CD (2015a) Climate warming and agricultural stressors interact to determine stream periphyton community composition. Global Change Biology, **21**, 206-222.

Piggott JJ, Townsend CR, Matthaei CD (2015b) Climate warming and agricultural stressors interact to determine stream macroinvertebrate community dynamics. Global Change Biology, **21**, 1887-1906.

Poff NL, Hart DD (2002) How dams vary and why it matters for the emerging science of dam removal. Bioscience, **52**, 659-668.

Poulsen BO (2002) Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. Biodiversity and Conservation, **11**, 1551-1566.

Pringle CM, Naiman RJ, Bretschko G *et al.* (1988) Patch dynamics in lotic ecosystems: The stream as a mosaic. Journal of the North American Benthological Society, **7**, 503-524.

R Core Development Team (2013) R: A language and environment for statistical computing. R foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/.

Reid SM, Carl LM, Lean JL (2005) Influence of riffle characteristics, surficial geology, and natural barriers on the distribution of the channel darter, Percina copelandi, in the Lake Ontario basin. Environmental Biology of Fishes, **72**, 241-249.

Ricketts TH (2001) The matrix matters: Effective isolation in fragmented landscapes. American Naturalist, **158**, 87-99.

Rincón PA (1999) Uso do micro-hábitat em peixes de riachos: métodos e perspectivas, p. 23-90. *In* Caramaschi EP, Mazzoni R, Peres-Neto PR (eds.). Ecologia de peixes de Riachos. Série Oecologia Brasiliensis, Rio de Janeiro, Brasil.

Rosseel Y (2012) lavaan: An R package for structural equation modeling. Journal of Statistical Software, **48**, 1–36.

Rüdisser J, Walde J, Tasser E, Fruhauf J, Teufelbauer N, Tappeiner U (2015) Biodiversity in cultural landscapes: influence of land use intensity on bird assemblages. Landscape Ecology, **30**, 1851-1863.

Schaefer J (2001) Riffles as barriers to interpool movement by three cyprinids (Notropis boops, Campostoma anomalum and Cyprinella venusta). Freshwater Biology, **46**, 379-388.

Scheiner SM, Chiarucci A, Fox GA, Helmus MR, Mcglinn DJ, Willig MR (2011) The underpinnings of the relationship of species richness with space and time. Ecological

Monographs, **81**, 195-213.

Schlosser IJ (1982) Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs, **52**, 395-414.

Schlosser IJ (1987) The role of predation in age-related and size-related habitat use by stream fishes. Ecology, **68**, 651-659.

Schlosser IJ (1995) Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia, **303**, 71-81.

Schwartz JS, Herricks EE (2008) Fish use of ecohydraulic-based mesohabitat units in a low-gradient Illinois stream: implications for stream restoration. Aquatic Conservation-Marine and Freshwater Ecosystems, **18**, 852-866.

Schwartz JS (2016) Use of Ecohydraulic-Based Mesohabitat Classification and Fish Species Traits for Stream Restoration Design. Water, **8**.

Shafer CL (1990) Nature reserves: island theory and conservation practice. Smithsonian Institution Press, Washington, DC

Shirk AJ, Raphael MG, Cushman SA (2014) Spatiotemporal variation in resource selection: insights from the American marten (Martes americana). Ecological Applications, **24**, 1434-1444.

Starks TA, Long JM, Dzialowski AR (2016) Community Structure of Age-0 Fishes in Paired Mainstem and Created Shallow-water Habitats in the Lower Missouri River. River Research and Applications, **32**, 753-762.

Steffan-Dewenter I (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conservation Biology, **17**, 1036-1044.

Strauch AM, Mackenzie RA, Giardina CP, Bruland GL (2015) Climate driven changes to rainfall and streamflow patterns in a model tropical island hydrological system. Journal of Hydrology, **523**, 160-169.

Stanley EH, Luebke MA, Doyle MW, Marshall D. (2002) Short-term changes in channel form and macroinvertebrate communities following low-head dam removal. Journal of the North American Benthological Society, **21**, 172–187.

Taylor CM (2000) A large-scale comparative analysis of riffle and pool fish communities in an upland stream system. Environmental Biology of Fishes, **58**, 89-95.

Teichert N, Valade P, Bosc P, Richarson M, Gaudin P (2013) Spawning-habitat selection of an Indo-Pacific amphidromous gobiid fish, Sicyopterus lagocephalus (Pallas). Marine and Freshwater Research, **64**, 1058-1067.

Teresa FB, Casatti L (2012) Influence of forest cover and mesohabitat types on functional and taxonomic diversity of fish communities in Neotropical lowland streams. Ecology of Freshwater Fish, **21**, 433-442.

Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography, **31**, 79-92.

Tiemann JS (2014) Ozark logperch, *Percina fulvitaenia* Morris and Page 1981. Pages 422-423 *In* Kansas Fishes Committee. Kanas Fishes. University Press of Kansas, Lawrence, KS.

Turner MG, Gardner RH, O'Neill RV (2001) Landscape ecology in theory and practice. Springer-Verlag, New York.

Vadas RL, Orth DJ (2000) Habitat use of fish communities in a Virginia stream system. Environmental Biology of Fishes, **59**, 253-269.

Vaughn CC (2010) Biodiversity Losses and Ecosystem Function in Freshwaters: Emerging
Conclusions and Research Directions. Bioscience, **60**, 25-35.

Villemey A, Van Halder I, Ouin A *et al.* (2015) Mosaic of grasslands and woodlands is more
effective than habitat connectivity to conserve butterflies in French farmland. Biological
Conservation, **191**, 206-215.

Wagner HH, Edwards PJ (2001) Quantifying habitat specificity to assess the contribution of a
patch to species richness at a landscape scale. Landscape Ecology, **16**, 121-131.

Wagner HH, Wildi O, Ewald KC (2000) Additive partitioning of plant species diversity in an
agricultural mosaic landscape. Landscape Ecology, **15**, 219-227.

Wasserman TN, Cushman SA, Shirk AS, Landguth EL, Littell JS (2012) Simulating the effects
of climate change on population connectivity of American marten (Martes americana) in
the northern Rocky Mountains, USA. Landscape Ecology, **27**, 211-225.

Weibull AC, Ostman O, Granqvist A (2003) Species richness in agroecosystems: the effect of
landscape, habitat and farm management. Biodiversity and Conservation, **12**, 1335-1355.

Wenny DG, Clawson RL, Faaborg J, Sheriff SL (1993) Population density, habitat selection and
minimum area requirements of three forest-interior warblers in Central Missouri. Condor,
95, 968-979.

Wiens JA (2002) Riverine landscapes: taking landscape ecology into the water. Freshwater
Biology, **47**, 501-515.

Wildhaber ML (2014) Neosho madtom, *Naturus placidus* Taylor 1969. Pages 303-305 *In* Kansas
Fishes Committee. Kanas Fishes. University Press of Kansas, Lawrence, KS.

Williams SE, Marsh H, Winter J (2002) Spatial scale, species diversity, and habitat structure:
Small mammals in Australian tropical rain forest. Ecology, **83**, 1317-1329.

Williams NM, Kremen C (2007) Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecological Applications, **17**, 910-921.

Winemiller KO, Jepsen DB (1998) Effects of seasonality and fish movement on tropical river food webs. Journal of Fish Biology, **53**, 267–296.

Wissmar RC, Craig SD (2004) Factors affecting habitat selection by a small spawning charr population, bull trout, Salvelinus confluentus: implications for recovery of an endangered species. Fisheries Management and Ecology, **11**, 23-31.

Wu JG, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. Quarterly Review of Biology, **70**, 439-466.

Wyrick JR, Pasternack GB (2014) Geospatial organization of fluvial landforms in a gravel-cobble river: Beyond the riffle-pool couplet. Geomorphology, **213**, 48-65.

Yarnell SM (2005) Spatial heterogeneity of *Rana boyli*i habitat: physical processes, quantification and ecological meaningfulness. PhD dissertation, University of California, Davis.

Yeiser JM, Richter SC (2015) Microhabitat conditions influence mesohabitat associations and distribution of larval salamanders in headwater streams. Hydrobiologia, **751**, 175-187.

Zhao T, Grenouillet G, Pool T, Tudesque L, Cucherousset J (2016) Environmental determinants of fish community structure in gravel pit lakes. Ecology of Freshwater Fish, **25**, 412-421.

Figure 3.1. Conceptual diagram outlining (I) types of configurational heterogeneity and (II) specific research questions linking configurational heterogeneity metrics with biodiversity.

I. Types of Spatial Heterogeneity

Q1 Are habitat patches discrete and does the arrangement of patches differ across riverscape mosaics?

(a) Habitat type   **(b)** Habitat amount   **(c)** Habitat arrangement

(d) Increasing configurational heterogeneity
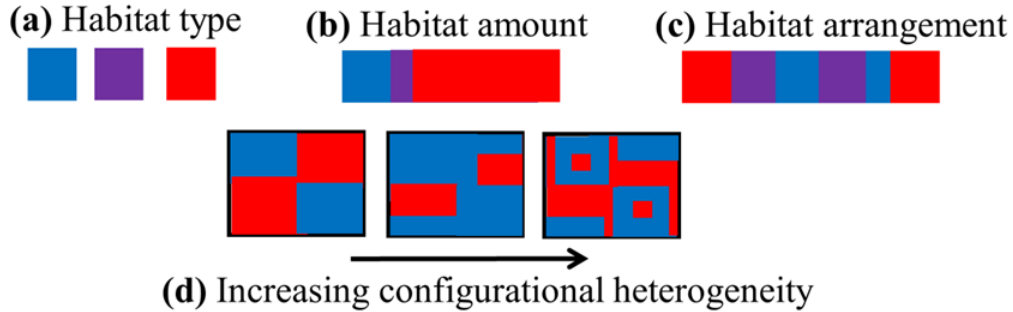
II. Questions on Configurational Heterogeneity

Q2. Do habitat characteristics within riffle habitat influence fish biodiversity?

$\uparrow$ Depth / Velocity $=$ $\uparrow$ Species richness
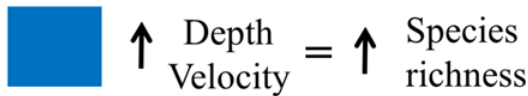
Q3. Where are the high biodiversity habitats located?

Q4 How do configurational heterogeneity metrics relate to biodiversity?

(a) Size   **(b) Shape**

(c) Patch density

Target patch $\downarrow$ Low patch density $\uparrow$ High patch density
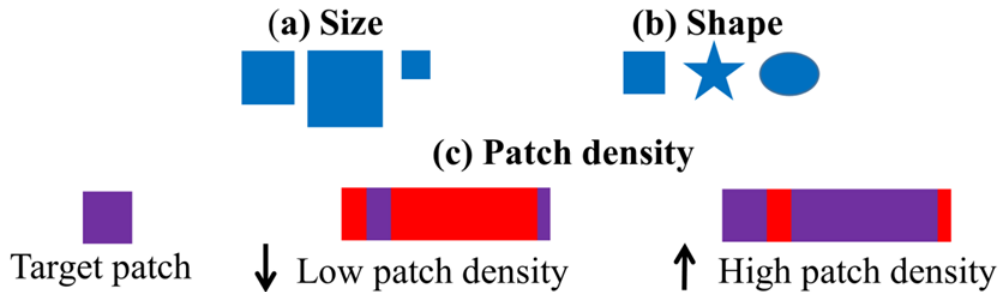
Q5 Do adjacent habitats influence habitat characteristics and biodiversity?

(a) Habitat   **(b) Biodiversity**

$\uparrow$ Depth $\uparrow$ Velcoity $\uparrow$ Species richness

128
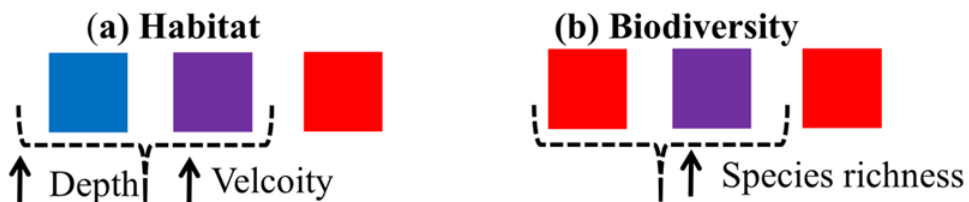
Figure 3.2. Map of study area representing ten sampling sites located along the Neosho and Cottonwood Rivers, KS. Black dots represent low-head dam sites and gray dots undammed sections of the rivers.
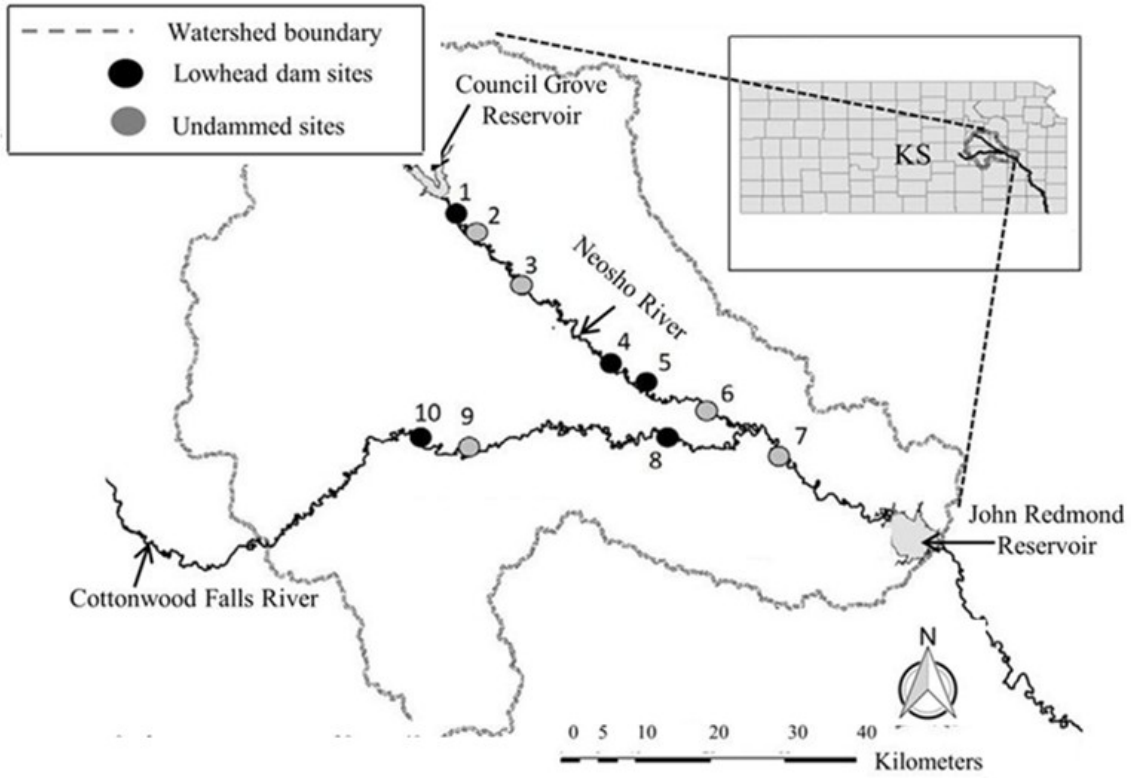
Figure 3.3. Non-metric multidimensional scaling biplot for stream habitats (glide, pool, riffle, and run) at ten sample sites located along the Neosho and Cottonwood Rivers, KS. Dots represent each habitat sample (N = 142). Ellipses indicate 95% confidence ellipses (group centroids) for the mean. Analysis of similarity indicates significant separation among each habitat type (ANOSIM Global R = 0.30, p < 0.001).
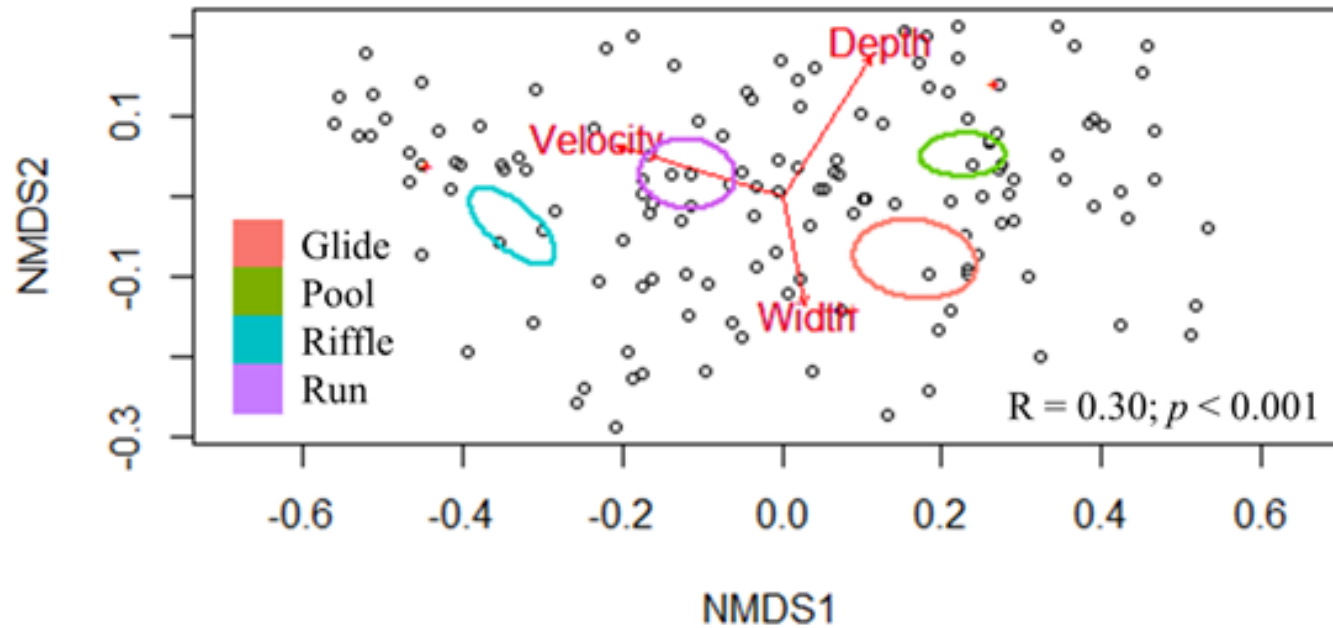
Figure 3.4. Longitudinal profiles for each of ten sampling location along the Neosho and Cottonwood Rivers, KS. Sampling occurred for 3km at each site. Represented are mean patch area, total number of habitat patches (N), and overall habitat diversity calculated using Shannon's Diversity Index (H') for pool, riffle, run, and glide habitats.
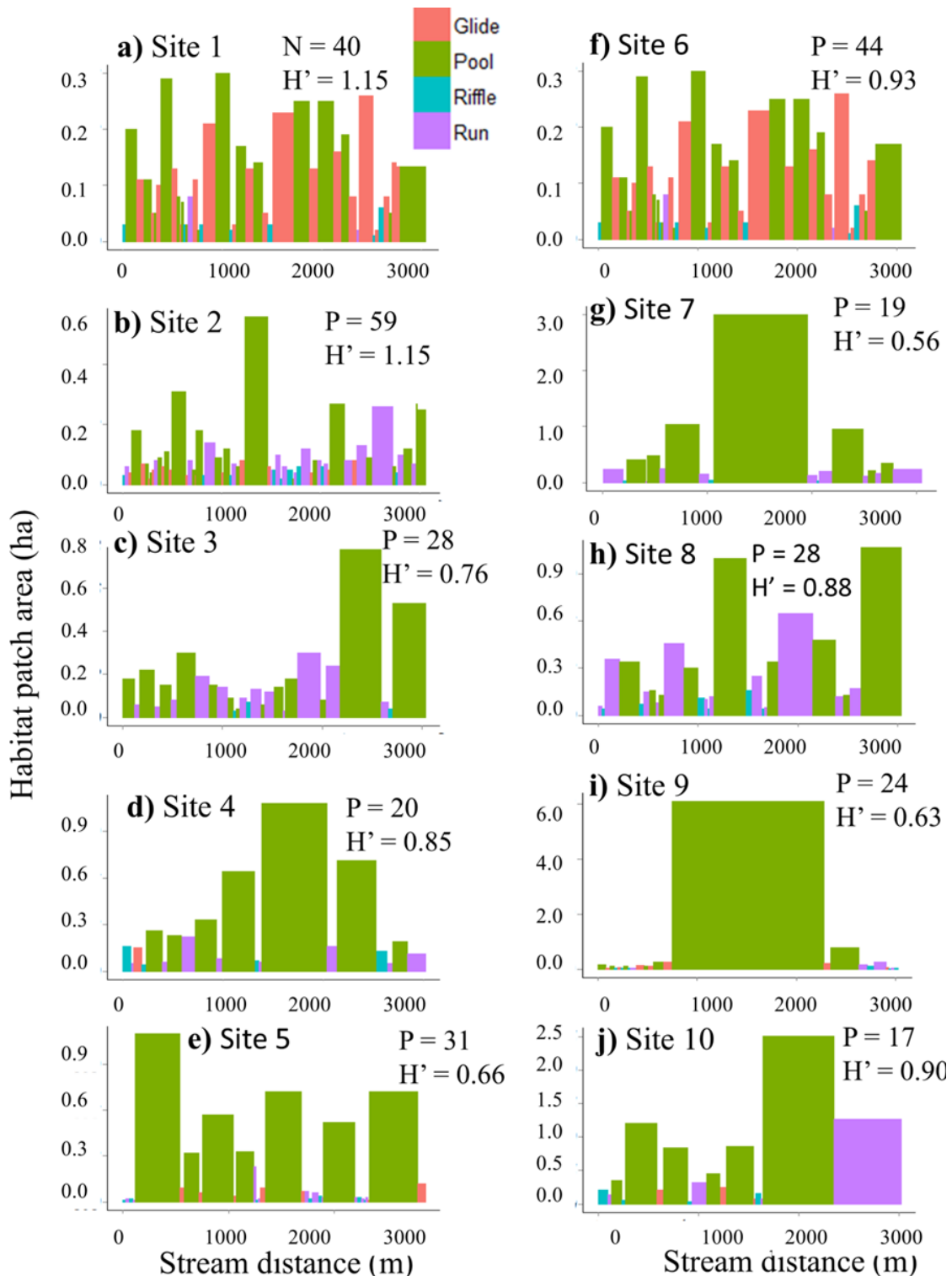
Figure 3.5. Linear regressions between species richness and a) stream depth and b) stream flow velocity within all riffle habitats sampled in the Upper Neosho River Basin. Arrows indicate locations of riffles with the highest biodiversity (upper 33% of all riffles sampled) based upon regressions for c) stream depth and d) stream flow velocity.
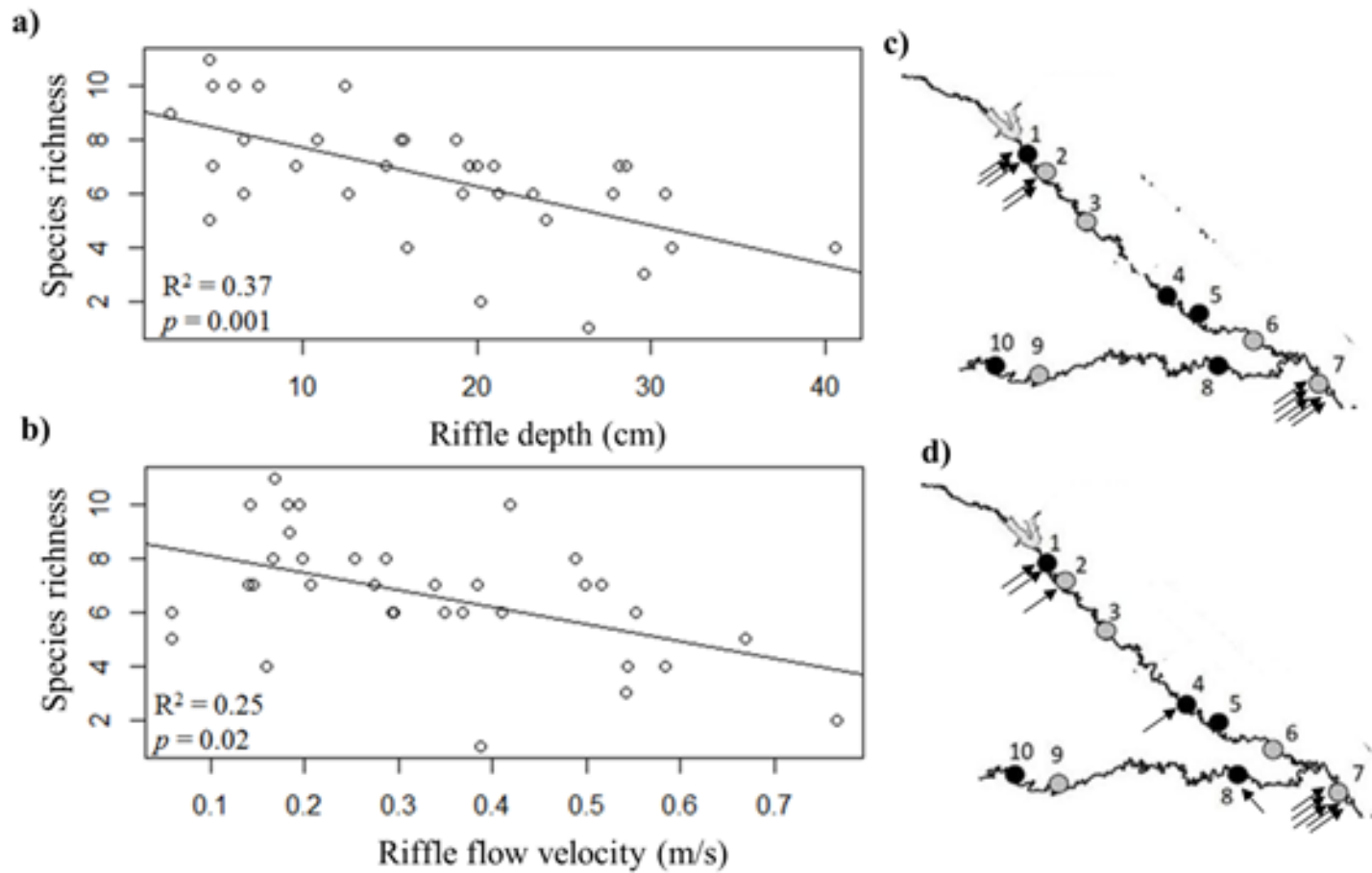
Figure 3.6. Boxplots showing significant relationships of within habitat characteristics relative to adjacent habitats: a) illustrates how flow velocity within pool habitats is influenced by downstream adjacent habitats, b) illustrates how depth within run habitats is influenced by upstream adjacent habitats, a) illustrates how flow velocity within glide habitats is influenced by downstream adjacent habitats, b) illustrates how depth within riffle habitats is influenced by upstream adjacent habitats. Heavy horizontal lines depict the median, the box represents the 2nd and 3rd quartiles, and the whiskers show the 1st and 4th quartiles.
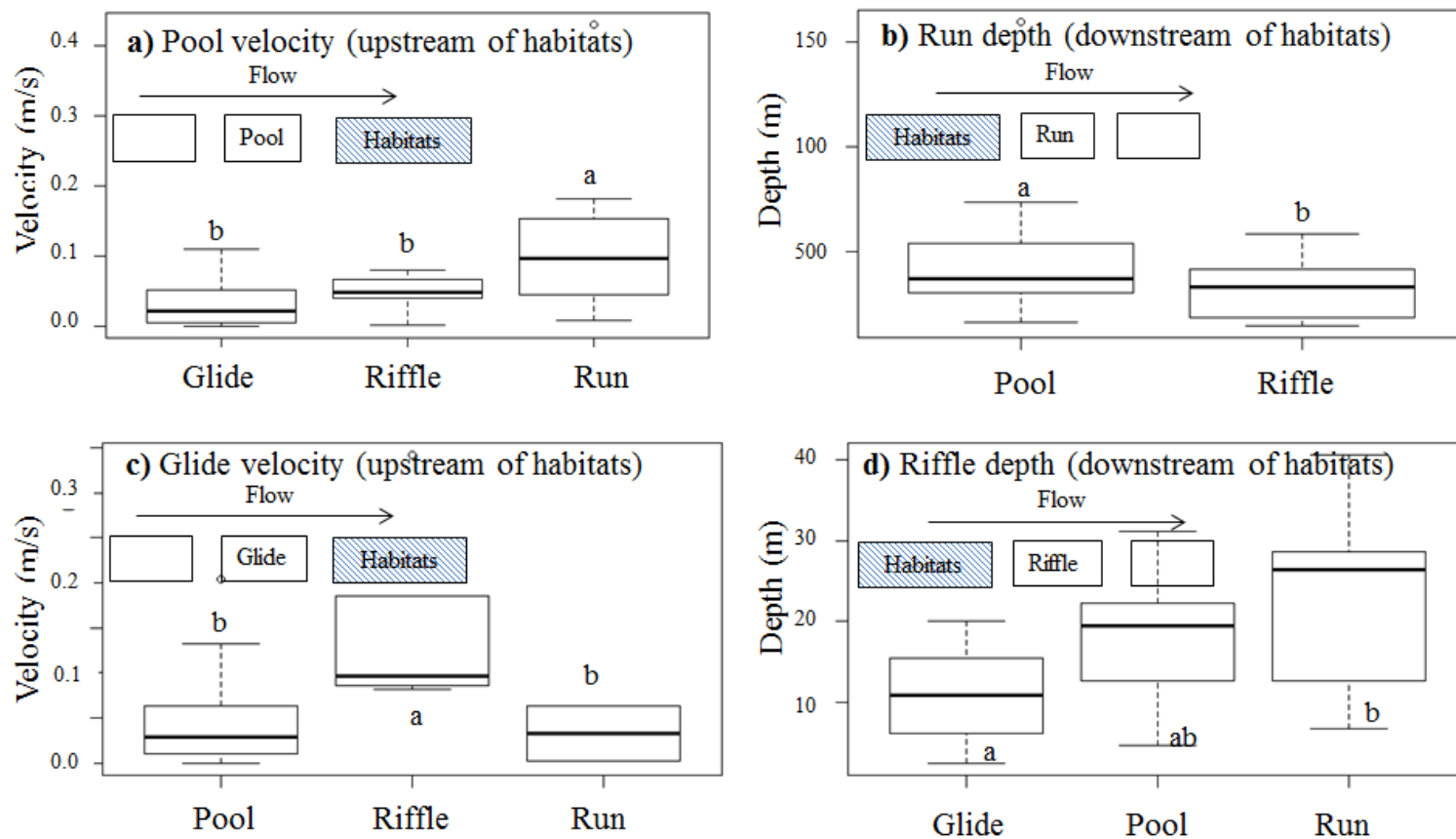
Figure 3.7. Path analyses investigating direct and indirect relationships for species richness a) within riffle habitats that were located immediately downstream of glides b) within riffle habitats that were located immediately downstream of runs and c) within riffle habitats that were located immediately upstream of glides. We only show significant relationships at α = 0.05. Solid lines represent positive relationships and dashed lines represent negative relationships. The standardized slope (β), coefficient of determination (R2), and significance (p) are shown for each variable pair (i.e., over each connecting line).
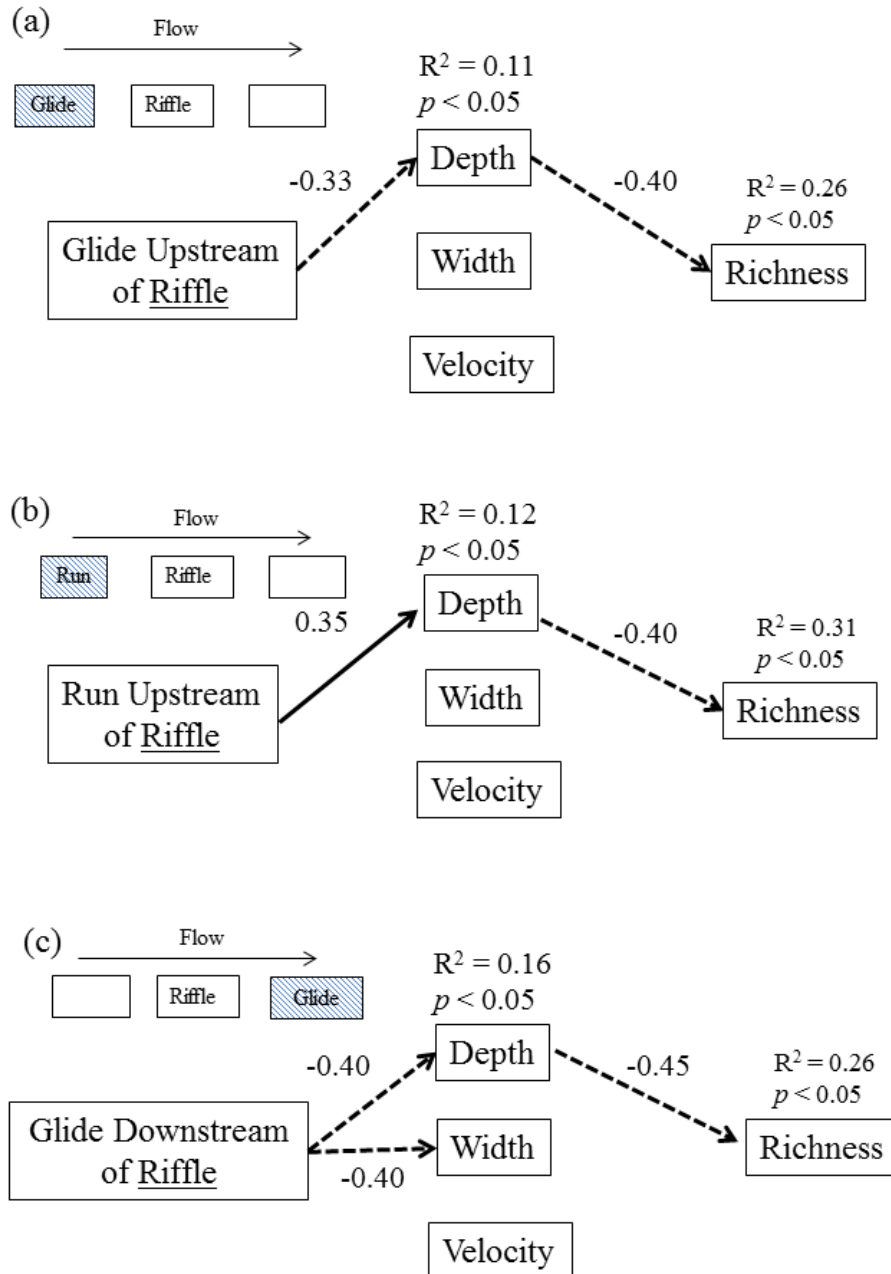
Table 3.1. Multiple regression models to examine relationships between species richness (response) and configurational heterogeneity metrics (predictor). Bolded denotes significant variables at α = 0.05 and () displays standard errors. Abbreviations include the following: par = perimeter-area ratio, df = degrees of freedom, vif = variance inflation factor. Model average was calculated as the mean slope for each predictor. Variable importance was calculated as the proportion of candidate models for which each predictor was included.

Model	Riffle patch density	% Variation Explained	Riffle Area	% Variation Explained	Glide Area	% Variation Explained	Riffle perimeter-area ratio	% Variation Explained	Run Area	% Variation Explained	Model R square	p	df	AICc	Δ AICc	weight	vif
Riffle patch density + Riffle area	**3.15** **(0.64)**	76.64	**1.96** **(0.64)**	23.36							0.75	0.004	4	53.2	0	0.28	1.07
Riffle patch density + Glide area	**2.17** **(0.66)**	54.32			**1.93** **(0.66)**	45.68					0.73	0.004	4	53.7	0.44	0.23	1.07
Riffle patch density + Riffle par	**3.26** **(0.69)**	80.27					**-1.91** **(0.69)**	19.73			0.71	0.005	4	54.3	1.06	0.17	1.11
Riffle patch density + Run area	**3.98** **(0.85)**	84.75							**2.19** **(0.85)**	15.25	0.69	0.007	4	55.1	1.88	0.11	1.57
Model average	14 (0.7	74.00	959 (0.6	23.36	93 (0.6	45.68	(0.69)	19.73	(0.85)	15.25							
Variable importance	1.00		0.25		0.25		0.25		0.25								

Appendix A - Fish Sampling Data

Table A.1

Total abundance, percentage of total fish captured, and total tow occurrence for species collected at ten sample sites located within the Neosho and Cottonwood Rivers, KS. Fish were categorized into two groups, common fish (captured at ≥ 85% of total sites sampled) and uncommon fish (captured at < 15% of total sites sampled).

Common Name	Scientific Name	Abundance N	Abundance %	Occurrence %
		A. Common Fish		
Red Shiner	Cyprinella *lutrensis*	4,641	59.6	94.0
Sand Shiner	Notropis *stramineus*	722	9.3	56.9
Bullhead Minnow	Pimephales *vigiliax*	523	6.7	85.3
Mimic Shiner	N. *volucellus*	387	5.0	40.5
Slenderhead Darter	Percina *phoxocephala*	289	3.7	66.4
Orangespotted Sunfish	Lepomis *humilis*	271	3.5	37.1
Central Stoneroller	Campostoma *anomalum*	265	3.4	25.9
Suckermouth Minnow	Phenacobius *mirabilis*	204	2.6	34.5
Bluntnose Minnow	P. *notatus*	128	1.6	25.0
Fantail Darter	Etheostoma *flabellare*	109	1.4	12.9
Bluntface Shiner	C. *camura*	66	0.9	18.1
Longear Sunfish	L. *megalotis*	44	0.6	25.0
		B. Uncommon Fish		
Orangethroat Darter	E. *spectabile*	11	< 0.3	5.2
Freckled Madtom	Noturus *nocturnus*	5	< 0.3	3.4
Neosho Madtom	N. *placidus*	4	< 0.3	1.7
Slender Madtom	N. *exilis*	1	< 0.3	0.9
Stonecat	N. *flavus*	1	< 0.3	0.9
Fathead Minnow	P. *promelas*	8	< 0.3	4.3
Brook Silverside	Labidesthes *sicculus*	6	< 0.3	2.6
White Crappie	Pomoxis *annularis*	5	< 0.3	3.4
Gizzard Shad	Dorosoma *cepedianum*	4	< 0.3	3.4
Redfin Shiner	Lythrurus *umbratilis*	4	< 0.3	2.6
Largemouth Bass	Micropterus *salmoides*	3	< 0.3	2.6
Flathead Catfish	Pylodictis *olivaris*	3	< 0.3	2.6
Channel Darter	P. *copelandi*	3	< 0.3	2.6
Spotted Bass	M. *punctulatus*	2	< 0.3	1.7
Bluegill Sunfish	L. *macrochirus*	1	< 0.3	0.9
Green Sunfish	L. *cyanellus*	1	< 0.3	0.9
Smallmouth Bass	M. *dolomieu*	1	< 0.3	0.9
Ghost Shiner	N. *buchanani*	22	< 0.3	1.7
Channel Catfish	Ictalurus *punctatus*	20	< 0.3	2.6
Logperch	P. *caprodes*	15	< 0.3	3.4
Carmine Shiner	N. *percobromus*	10	< 0.3	1.7
Slim Minnow	P. *tenellus*	8	< 0.3	0.9
Golden Redhorse	Moxostoma *erythrurum*	4	< 0.3	0.9
TOTAL		7791	100	

Appendix B - Fish Habitat Guilds

Table B.1

Guilds of species collected at 10 sampling sites located within the Neosho and Cottonwood Rivers, KS based upon total abundance, proportion of abundance within each habitat (pool, riffle, run), and site occurrence of total abundance. Common fish were captured at ≥ 85% of total sites sampled. Uncommon fish (< 15% occurrence) were placed into guilds based upon the current literature.

| Common Name	Scientific Name	Abundance N	Abundance %	Occurrence %	Guild	Proportion of Abundance Pool	Riffle	Run
			A. Common Fish					
Central Stoneroller	Campostoma *anomalum*	265	3.4	25.9	Riffle Specialist	0.03	0.95	0.02
Suckermouth Minnow	Phenacobius *mirabilis*	204	2.6	34.5		0.04	0.85	0.11
Orangespotted Sunfish	Lepomis *humilis*	271	3.5	37.1	Pool Specialist	0.79	0.03	0.18
Bluntnose Minnow	Pimephales *notatus*	128	1.6	25.0	Riffle Generalist	0.18	0.56	0.26
Longear Sunfish	L. *megalotis*	44	0.6	25.0	Pool Generalist	0.7	0.07	0.23
Red Shiner	Cyprinella *lutrensis*	4,641	59.6	94.0	Riffle-Run Generalist	0.1	0.56	0.34
Bluntface Shiner	C. *camura*	66	0.9	18.1		0.06	0.62	0.32
Sand Shiner	Notropis *stramineus*	722	9.3	56.9	Pool-Run Generalist	0.32	0.1	0.58
Mimic Shiner	N. *volucellus*	387	5.0	40.5		0.32	0.1	0.58
Bullhead Minnow	P. *vigiliax*	523	6.7	85.3	Generalist	0.44	0.22	0.34
Slenderhead Darter	Percina *phoxocephala*	289	3.7	66.4		0.23	0.48	0.29
			B. Uncommon Fish					
Fantail Darter	Etheostoma *flabellare*	109	1.4	12.9	Riffle Specialist			
Orangethroat Darter	E. *spectabile*	11	< 0.3	5.2				
Freckled Madtom	Noturus *nocturnus*	5	< 0.3	3.4				
Neosho Madtom	N. *placidus*	4	< 0.3	1.7				
Slender Madtom	N. *exilis*	1	< 0.3	0.9				
Stonecat	N. *flavus*	1	< 0.3	0.9				
Fathead Minnow	P. *promelas*	8	< 0.3	4.3	Pool Specialist			
Brook Silverside	Labidesthes *sicculus*	6	< 0.3	2.6				
White Crappie	Pomoxis *annularis*	5	< 0.3	3.4				
Gizzard Shad	Dorosoma *cepedianum*	4	< 0.3	3.4				
Redfin Shiner	Lythrurus *umbratilis*	4	< 0.3	2.6				
Largemouth Bass	Micropterus *salmoides*	3	< 0.3	2.6				
Flathead Catfish	Pylodictis *olivaris*	3	< 0.3	2.6				
Channel Darter	P. *copelandi*	3	< 0.3	2.6				
Spotted Bass	M. *punctulatus*	2	< 0.3	1.7				
Bluegill Sunfish	L. *macrochirus*	1	< 0.3	0.9				
Green Sunfish	L. *cyanellus*	1	< 0.3	0.9				
Smallmouth Bass	M. *dolomieu*	1	< 0.3	0.9				
Ghost Shiner	N. *buchanani*	22	< 0.3		Pool-Run Generalist			
Channel Catfish	Ictalurus *punctatus*	20	< 0.3					
Logperch	P. *caprodes*	15	< 0.3					
Carmine Shiner	N. *percobromus*	10	< 0.3					
Slim Minnow	P. *tenellus*	8	< 0.3					
Golden Redhorse	Moxostoma *erythrurum*	4	< 0.3					
TOTAL		7791	100					

Table B.2

SIMPER results for fish data sets on A) abundance, B) presence/absence, and C) guilds including habitat specific abundance and cumulative sum explained (>0.05).

| Habitat Comparison	Species	(a) Mean Abund.	(b) Mean Abund.	Cum. Sum	Δ Cum. Sum
(a) Abundance					
Pool (a)-Riffle (b)	Red Shiner	9.70	76.30	0.55	0.55
	Central Stoneroller	0.19	7.40	0.62	0.07
	Bullhead Minnow	4.90	3.40	0.67	0.05
	Orangespotted Sunfish	4.57	0.24	0.72	0.05
	Suckermouth Minnow	0.19	5.09	0.77	0.05
Pool (a)-Run (b)	Red Shiner	9.70	46.70	0.46	0.46
	Sand Shiner	4.85	12.41	0.59	0.13
	Bullhead Minnow	4.90	5.30	0.69	0.10
	Orangespotted Sunfish	4.57	1.41	0.77	0.08
	Mimic Shiner	5.47	2.88	0.84	0.07
Riffle (a) - Run (b)	Red Shiner	76.30	46.70	0.54	0.54
	Sand Shiner	2.12	12.41	0.62	0.08
	Central Stoneroller	7.40	0.15	0.69	0.07
	Bullhead Minnow	3.40	5.30	0.76	0.07
	Suckermouth Minnow	5.09	0.65	0.81	0.05
(b) Presence/Absence					
Pool (a)-Riffle (b)	Suckermouth Minnow	0.09	0.76	0.10	0.10
	Central Stoneroller	0.09	0.68	0.20	0.10
	Orangespotted Sunfish	0.57	0.12	0.29	0.09
	Slenderhead Darter	0.55	0.82	0.37	0.08
	Sand Shiner	0.49	0.50	0.44	0.07
Pool (a)-Run (b)	Sand Shiner	0.49	0.76	0.10	0.10
	Orangespotted Sunfish	0.57	0.35	0.19	0.09
	Slenderhead Darter	0.55	0.68	0.28	0.09
	Mimic Shiner	0.49	0.41	0.37	0.09
	Longear Sunfish	0.38	0.26	0.45	0.08
Riffle (a) - Run (b)	Central Stoneroller	0.68	0.09	0.10	0.10
	Suckermouth Minnow	0.76	0.29	0.20	0.10
	Sand Shiner	0.50	0.76	0.29	0.09
	Mimic Shiner	0.29	0.41	0.36	0.07
	Slenderhead Darter	0.82	0.68	0.43	0.07
(c) Guild Abundance					
Pool (a)-Riffle (b)	Riffle Run Generalist	9.83	77.53	0.61	0.61
	Riffle Specialist	0.47	15.65	0.77	0.16
	Generalist	6.32	7.44	0.85	0.08
	Pool Run Generalist	6.34	1.12	0.91	0.06
	Pool Specialist	5.00	0.44	0.97	0.06
Pool (a)-Run (b)	Riffle Run Generalist	9.83	47.32	0.56	0.56
	Generalist	6.31	7.71	0.70	0.14
	Pool Run Generalist	6.34	3.82	0.82	0.12
	Pool Specialist	5.00	1.82	0.93	0.11
Riffle (a) - Run (b)	Riffle Run Generalist	77.53	47.32	0.62	0.62
	Riffle Specialist	15.64	1.35	0.79	0.17
	Generalist	7.44	7.71	0.89	0.10
	Pool Run Generalist	1.12	3.82	0.94	0.05

Figure B.1

Bar plots showing relative proportion (primary Y-axis – black bar) and mean abundance (secondary Y-axis- gray bar) within each habitat (pool, riffle, and run). Empirically derived habitat guilds are shown for each species. Data are mean and SE. Fish examples include (a) Suckermouth Minnow, (b) Orangespotted Sunfish, (c) Bluntnose Minnow, (d) Longear Sunfish, (e) Red Shiner, (f) Sand Shiner, and (g) Bullhead Minnow. We used a hierarchical agglomerative cluster analysis (h) with average linkage and Euclidean distance matrix of the proportions as an alternate way to create guild classifications.
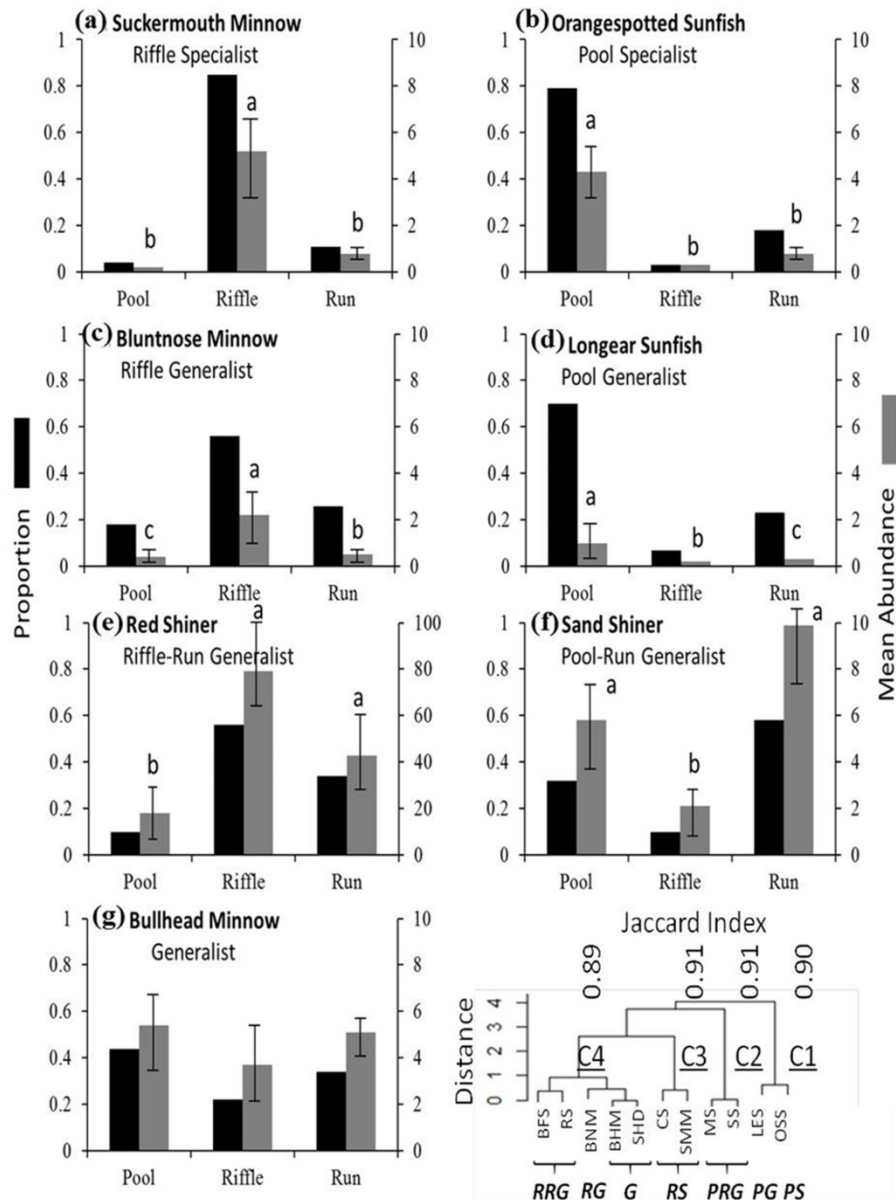
Figure B.2

Plot of SIMPER results for influential fish species from fish-habitat guilds based on (A-E) mean abundance (Y axis) for the abundance data set and (F-J) proportion (Y axis) for the presence-absence datasets. Data are means. Guilds include (a, f) Riffle specialist, (b, g) Pool specialist, (c) Riffle-run generalist, (d, i) Pool-run generalist, (e, j) Generalist, and (h) Pool generalist. Numbers indicate the cumulative sum explained per fish species between each set of habitats.

140
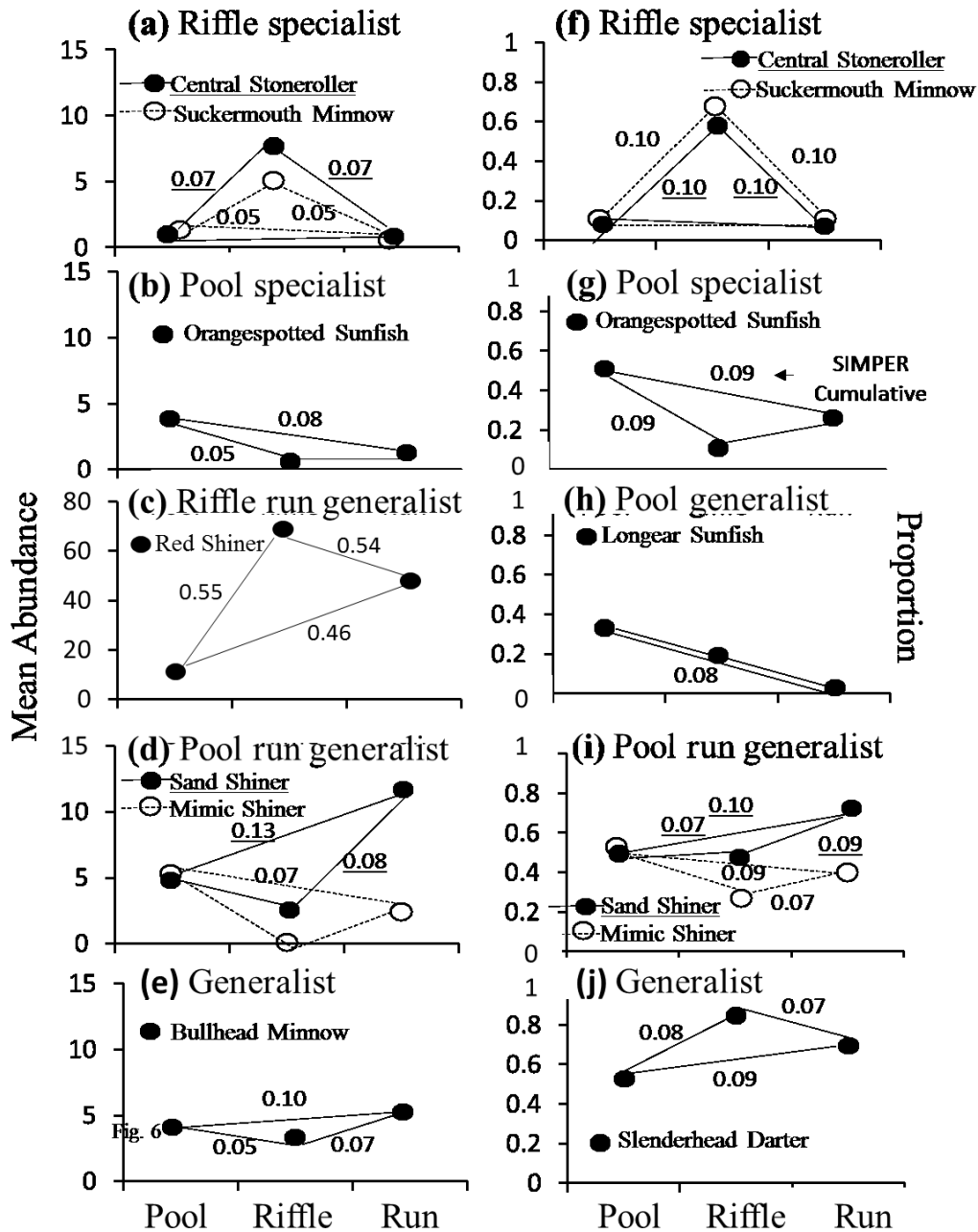
Appendix C - Correlation Table for Landscape Metrics

Table C.1

Correlation table for landscape metrics used in Chapter 3. Correlations were examined between each habitat type (pool = P, riffle = Ri, Glide = G, Run = Ru) and landscape metric (mean patch size = AREA, perimeter-area ratio = PARA, patch density = PD). Significant correlations (> 0.70) are shown in bold.

	P_PD	P_AREA	P_PARA	Ri_PD	Ri_AREA	Ri_PARA	G_PD	G_AREA	G_PARA	Ru_PD	Ru_AREA	Ru_PARA
P_PD		**-0.84**	**0.79**	0.36	-0.42	0.05	0.61	-0.27	0.43	0.54	-0.45	0.00
P_AREA			**-0.81**	-0.61	0.21	0.03	-0.56	0.21	-0.29	-0.51	0.56	-0.28
P_PARA				0.53	-0.34	0.01	0.58	0.03	0.47	0.34	**-0.71**	0.06
Ri_PD					-0.25	0.31	**0.75**	0.26	0.59	0.02	-0.60	0.26
Ri_AREA						-0.67	-0.39	0.51	-0.28	-0.16	0.68	-0.19
Ri_PARA							0.24	-0.19	0.37	-0.04	-0.52	0.35
G_PD								0.31	**0.88**	-0.18	-0.48	-0.01
G_AREA									0.52	-0.63	0.20	-0.39
G_PARA										-0.31	-0.41	-0.05
Ru_PD											-0.23	0.16
Ru_AREA												-0.37
Ru_PARA												