Article type : Feature

Feature

Does Type, Quantity, and Location of Habitat Matter for Fish Diversity in a Great Plains Riverscape?

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Abstract

Fisheries professionals frequently measure habitat type and amount, but less often measure the importance of where those habitats are located and in what combinations. We address this challenge by testing whether the individual and combined type, quantity, and location of habitat affects fish diversity in the upper Neosho River basin, Kansas, as a different approach to measuring habitat heterogeneity. Habitat type mattered in that species richness increased in areas of higher riffle density. Furthermore, variation within habitat type also influenced fish diversity; specifically, slower, shallower riffles had more species of fish. The spatial arrangement (i.e.,

impact of neighbor habitats) influenced fish diversity patterns in that riffle–run and riffle–glide pairings altered riffle habitat characteristics. The study illustrates a useful approach by measuring the type, amount, and arrangement of habitats to assess fish populations and could be adapted to other stream ecosystems.

INTRODUCTION

The call to apply landscape approaches to aquatic systems (Wiens 2002; Datry et al. 2016) underscores the need for researchers to address how patterns of organismal and resource heterogeneity affect basic and applied problems in natural and impacted aquatic ecosystems. For streams, collecting habitat and taxonomic data at multiple spatial scales are important (Fausch et al. 2002). Specifically, many fisheries professionals are interested in collecting, analyzing, and interpreting ecological data at larger geographic extents and would benefit from a better understanding of aquatic landscapes. Nontraditional examinations of fish distribution data within aquatic landscapes (e.g., innovative or modified metrics) that address key questions relevant to aquatic systems to solve persistent fisheries problems are needed. Our purpose was to measure patterns of heterogeneity and assess habitat arrangement on fish diversity to fill gaps in applied problem solving for aquatic landscapes.

Lotic ecosystems are defined by the spatial and temporal hierarchy of biological and physical characteristics along the network (Vannote et al. 1980; Frissell et al. 1986; Montgomery 1999). Strong associations have been found between fish assemblages (e.g., individual species, richness, trophic structure) and large-scale features that include position within stream network (Smith and Kraft 2005), catchment area (Osborne and Wiley 1992; Newall and Magnuson 1999), catchment shape (Chiu et al. 2020), and landuse (Allan et al. 1997; Wenger et al. 2008). Other have found that local environmental factors (e.g., instream habitat, water quality) are just as important at predicting fish assemblage structure (Meador and Goldstein 2003; Rowe et al. 2009; Hitchman et al. 2018a). While empirical investigations have been mixed, it is likely that multiple factors operate at various scales to structure stream fish assemblages (Fausch et al. 2002; Walters et al. 2009). For example, both landscape-scale (e.g., watershed landcover) and local-scale (e.g., substrate composition, woody debris) factors were important to explaining stream fish assemblage structure in central Texas river basins (Pease et al. 2011). These along with many other studies exploring fish assemblage structure at local and basin-wide scales have yielded important insights. However, a need exists to perceive streams not as lines on a map, individual sampling points, or longitudinal gradients, but as spatially continuous, dynamic mosaics (Fausch et al. 2002).

While work has been done examining fish assemblage structure at local and basin-wide scales, much less has been done at intermediate scales (e.g., ~ 10^2–10^5 m). Processes operating at these scales are often critical life-history events for many fishes (Fausch et al. 2002). To conceptualize streams as longitudinal and latitudinal mosaics, aquatic researchers need to gain an understanding of patterns and processes operating at intermediate scales. Spatial habitat heterogeneity (i.e., the uneven distribution of habitats of various sizes, shapes, amount, and arrangement) is an ecologically important characteristic of all ecosystems and, as in terrestrial systems, patterns of physical habitat heterogeneity can vary in aquatic systems with spatial scale. At smaller scales, discrete stream habitats exist based upon physical habitat structure (Cheek et al. 2016). At larger scales, a mosaic of habitats along the stream channel can create complex physical patterns to which various landscape metrics might be applied (Hitchman et al. 2018a). Therefore, metrics for aquatic landscapes are needed that measure habitat type, quantity, shape and arrangement (Figure 1-I). While many studies have been used to examine the relationship between fish and habitat, to our knowledge, this is the first that seeks to understand how the arrangement of habitats influences fish diversity.

Our goal was to develop an integrated approach that measures heterogeneity with the spatial arrangement of habitats and relate to fish diversity. We ask four specific research questions related to habitat type (variation across and within), quantity (size, density), shape, and spatial arrangement (Figure 1-I). First, we tested if specific combinations of physical variables (i.e., stream width, depth, flow velocity) created discrete habitat types that together created different spatial arrangements within each study reach (Figure 1-II, Q1a–b). Second, we tested how variation *within* discrete habitat types influenced fish diversity (Figure 1-II, Q2). Even if discrete types of habitat exist, within-habitat variation in physical conditions can still influence fish diversity patterns. Third, we asked if fish diversity is correlated to three commonly used terrestrial landscape metrics: habitat size, shape, and density (Figure 1- II, Q3 a–c). Fourth, we asked if the arrangement of a habitat with neighboring habitats influenced environmental variables and fish diversity (e.g., does a riffle below a pool function differently than a riffle below a run; Figure 1-II, Q4 a–c).

MATERIALS AND METHODS

Study Area

Our study was conducted within the upper Neosho River Basin (UNRB), Kansas, along the Neosho and Cottonwood rivers, 2 fifth-order rivers (Figure 2). The UNRB drains approximately 7,770 km^2 upstream of the John Redmond Reservoir. The basin is bounded on the north by Council Grove Reservoir and on the west by Marion Reservoir. The rivers within the study area lie upon limestone and shale bedrock underneath alluvium (Jurack and Perry 2005). Landuse is primarily agricultural (corn, wheat, soybean) with narrow riparian zones adjacent to crop fields and streams that are primarily cottonwood forests. Stream width ranged from approximately 22m to 60m. The highest elevations within our study site were 371.5m above mean sea level within the Neosho River (Figure 2, Site 1) and 353.9 m above mean sea level within the Cottonwood River (Figure 2, Site 10). The lowest elevation within our study site occurred at Site 7 (324.9m; Figure 2, Site 7) downstream of the confluence of the Neosho and Cottonwood rivers. Mean annual discharge was 8.72 m^3/s (SE ± 0.94, United States Geological Survey [USGS] gage 07179730, 1963–2013) for the Neosho River and 24.55 m^3/s (SE ± 2.19, USGS gage 07182250, 1963–2013) for the Cottonwood River.

We mapped habitat within 10 sites to measure habitat heterogeneity (Figure 2). Each site was 3 km in length from upstream to downstream, within which we measured habitat type (pool, riffle, run, glide), variation within habitat type, and the number, size, and arrangement of habitats for each type. Sampling occurred during baseflow conditions (13.0–19.0 m^3/s; USGS gage 07182250).

The basin contains three larger reservoir dams (listed previously) and six smaller low-head dams (Figure 2). One low-head dam was not sampled due to lack of landowner permission. Elsewhere we reported that no direct and consistent statistical differences existed in number of habitats per type between dammed and undammed sample sites, thus we included all sites in each analysis (Hitchman et al. 2018a, 2018b).

Field Sampling

Habitat Types

From June–August 2013, we identified and mapped habitats (N=310) within each site based on agreement by two independent observers, using an objective series of stream channel morphology, surface flow, depth, and sediment composition criteria (McCain et al. 1990; Harvey and Clifford 2009; Supplemental Material, Appendix 1). Habitats were classified as pool, riffle, run, or glide (see Supplemental Material, Appendix 1 for description). We quantified the spatial location of each habitat using trackplots at 5-second intervals and waypoints at the upper and lower boundary from a handheld Garmin GPSmap76Cx (Garmin International, Olathe, Kansas). Trackplots and waypoints for each habitat were imported into ArcMap v. 10.2 (Esri, Redlands, California) where they were digitized into polygons and converted to raster format.

Habitat Characteristics

Environmental variables (i.e., wetted stream width, water depth, and flow velocity) were measured within five habitats for each type (pool, riffle, run, glide) at each sample site. At sites where less than five habitats for a particular type existed, all habitats of that type were sampled. Wetted stream width was recorded using a Nikon 8398 range finder (<1 m accuracy, range 3–200 m) at the midpoint of each habitat. 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, Colorado) Model 2000 flowmeter.

Fish Diversity Sampling

We captured fish using a two-person mini-Missouri trawl, which has been used to capture both small and large-bodied benthic fish (e.g., Fencl et al. 2017; Hitchman et al. 2018a). The mini-Missouri trawl caught the same or more numbers of species as a seine net and backpack electrofisher in a controlled gear experiment (Fencl et al. 2017). Fish were collected using a 2.4-m mini-Missouri trawl (Herzog et al. 2009) with 35-mm outer mesh and 3.2-mm inner mesh pulled from upstream to downstream for 30 m. Fish were sampled in 134 of the 310 habitats mapped (43.2%). Fish were counted, identified to species, then returned alive to the stream. Additional details on all methods are provided elsewhere (Hitchman et al. 2018a, 2018b).

Data Analysis

Question 1: Do discrete habitat types exist (a) and does the arrangement of habitats differ across sites (b)?

We used non-metric multidimensional scaling to evaluate if habitat types formed discrete groups based on the environmental variables (stream width, water depth, and flow velocity). For the non-metric multidimensional scaling, we used a Bray–Curtis distance matrix. Habitat types were factors, environmental variables were response variables. Confidence ellipses (95%) were plotted along with each habitat sample ($N = 138$) to visualize the relative location of each habitat type. We quantitatively tested separation among habitat types (pool, glide, run, riffle) with an analysis of similarity (ANOSIM). A p value < 0.05 indicated that the environmental variables were quantitatively discrete among habitat types.

Next, we used a series of longitudinal profile plots to illustrate variation in the diversity, sequence, and size of habitats within and across each of our ten 3-km sites. To create each longitudinal profile, the length (m) of each habitat was plotted sequentially from upstream to downstream (X axis). The area of each (ha) was plotted on the Y axis. Habitat length and area were calculated from raster files for each site using ArcMap v. 10.2. These longitudinal profiles visually illustrated habitat diversity. To quantify differences in habitat diversity, we calculated the number of habitats and overall habitat heterogeneity (Shannon's Diversity Index) for each site. We then used a chi-square test with 2,000 Monte Carlo simulations to assess if habitat heterogeneity varied significantly across sample sites. Note, all statistical analyses outlined here and below were run using R v.4.1 (R Core Team 2013).

Question 2: Does within-habitat type variation influence fish diversity?

To examine if continuous variation in environmental variables (width, depth, flow velocity) within-a habitat type (pool, riffle, run, glide) affected fish species diversity, we ran multiple linear regression models for each environmental variable (X axis) relative to species richness (Y axis) within each habitat type. Because we were examining the influence of habitat arrangement on fish communities (not comparing diversity metrics), we chose a single, common measure of diversity (species richness). Species richness is commonly used diversity metric in the ecological literature and in this study provides similar results to other diversity metrics (e.g., species evenness, beta diversity; Supplemental Material, Appendix 2).

Question 3: Do landscape ecology metrics predict riverscape-scale fish diversity?

We chose three commonly used landscape ecology metrics that describe habitat to examine their relationship with fish species richness. For each habitat type (pool, riffle, run, and glide), we calculated mean habitat size (size), habitat perimeter–area ratio (shape), and habitat density (arrangement) 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). Mean habitat size was calculated as the average area (km^2) of each habitat within a particular habitat type for each site. Perimeter–area ratio was calculated as the ratio of habitat perimeter to the habitat area. Habitat density was calculated as the total number of habitats per 100 ha. The metrics were chosen because they could be calculated from our dataset and have been shown to be ecologically meaningful in terrestrial ecology studies (Supplemental Material, Appendix 1).

We then used an inference–theoretic approach to select the top multiple regression models (AIC_c; Burnham and Anderson 2002; ΔAIC_c scores < 2; MuMin package; Bartoń 2013) that related predictor variables (habitat size, habitat shape, habitat density for all four habitat types) to the species richness response variable. Each independent variable was standardized so the mean equals zero. For parsimony, we limited each candidate model to one or two predictor variables. We eliminated collinear models (variance inflation factor >10 or condition index >30) and models with pairs of correlated ($r > 0.70$) predictor variables.

Question 4: Do adjacent habitats influence habitat-specific characteristics and fish diversity?

Neighboring habitats may affect fish community patterns. We tested the effect of adjacent habitat types (upstream or downstream) on the environmental characteristics (e.g., depth, water velocity) of the target habitat type. For example, we investigated how environmental variables within pool habitat (target) would change when a riffle was present (adjacent habitat) both upstream and downstream. To test this neighbor effect, we used a multivariate analysis of variance (MANOVA) in which all combinations of adjacent habitat both upstream and downstream ($N = 24$) were the treatments and environmental variables (stream width, depth, and flow velocity) for each target habitat (pool, riffle, run, and glide) were the response variables.

Next, we used path analysis to evaluate direct and indirect effects of neighboring habitats on environmental variables and species richness within a target habitat. Path analysis calculates path coefficients (standardized partial regression coefficients) that quantify direct and indirect effects. Direct effects are the coefficients between two variables connected by a path. Indirect effects are effects mediated through another variable (e.g., habitat). Path analysis was performed for all combinations of target habitats (pool, riffle, run, and glide) and adjacent habitats both upstream and downstream (library lavaan with function sem in R; Rosseel 2012). Standardized path coefficients (standardized β) indicated the strength of relationships and R^2 measured the amount of variation explained by specific sets of variables. For both the MANOVA and the path analysis, we ran all combinations of target and neighbor habitats, but we only present significant relationships.

RESULTS

Question 1a: Do discrete habitat types exist?

Based on width, depth, and flow velocity, all habitat categories (riffle, run, pool, and glide) were quantitatively distinct (ANOSIM Global R = 0.29, $p = 0.001$; Figure 4). No overlap existed among 95% confidence ellipses, indicating clear separation among habitat types. Although physically distinct, run and glide habitats had environmental conditions that were intermediate between pool and riffle habitat types (Figure 3).

Question 1b: Does the arrangement of habitats differ across sites?

Habitat arrangement differed across our sample sites (Figure 4). Specifically, the number and type of habitats varied across sites ($\chi^2 = 70.42$, $p < 0.001$; Figure 4). The total number of habitats per sample site ranged from 17 (Figure 4j, Site 10) to 59 (Figure 4b, Site 2). Pool, riffle, and run habitats were present across all sites, but glides were irregularly distributed and were most commonly associated with riffles and pools (i.e., adjacent to pools 68–74%; adjacent to riffles 19–21%). Overall, site-specific habitat diversity ranged from 0.56 (Figure 4g) to 1.15 (Figure 4a, b). As specific examples, Sites 1 and 2 were characterized as having a high number of total habitats (40 and 59, respectively) and high habitat diversity (1.15 and 1.15, respectively; Figure 4a, b), whereas Sites 7 and 9 had fewer total habitats (19 and 24, respectively) and low habitat diversity (0.56 and 0.63, respectively; Figure 4g, i).

Question 2: Does within-habitat variation influence fish diversity?

Variation in species richness existed within select habitat types. Within 143 unique habitats, we sampled a total of 7,791 fish representing 35 species, across 7 families, at 10 sites within the upper Neosho River sub-drainage. No significant relationships existed between fish species richness and within-habitat variation in environmental variables (width, depth, flow, flow velocity) for pools, glides, and runs (data not shown). However, for riffles, shallower ($F_{1,33}$ = 18.82; $p = 0.001$; Figure 5a) and slower ($F_{1,33}$ = 10.46; $p = 0.02$; Figure 5b) riffles had more fish species.

Question 3: Do landscape ecology metrics predict riverscape-scale fish diversity?

For three commonly used landscape ecology metrics (*habitat size, habitat shape, habitat density for four habitat types*), riffle *density* had the greatest influence on fish species richness (Table 1). The four top models ($\Delta AIC_c < 2$) were significant (p = 0.004–0.007) and had R^2 values of 0.69–0.75 (Table 1). In these top models, *riffle density* had a high and positive model-averaged standardized slope ($\beta = 3.14$), a high variable importance (VI = 1.0) and explained 54.3–84.8% (average 74%) of the variation in fish richness. Thus, sites with many riffles had a higher number of fish species.

As predicted, some habitat size metrics were also positively related to fish species richness in that individual models and sites with larger mean habitat sizes of riffles, glides, and runs had more fish species, with larger areas having a higher species richness (mean *riffle area* [$\beta = 2.0$; VI = 0.25; 23.4% of variance]; mean *glide area*. [$\beta = 1.9$; VI = 0.25; 45.7% of variance]; mean *run area* [$\beta = 2.2$; VI = 0.25; 15.3% of variance]; Table 1). Contrary to predictions from terrestrial systems that higher edge area would increase diversity, riffle Perimeter–area ($\beta = -1.9$; VI = 0.25; 19.7% of variance) was negatively related to fish species richness (Table 1).

Question 4: Do adjacent habitats influence habitat-specific characteristics and fish diversity?

Neighboring habitats altered environmental characteristics of target habitats, and, in some cases, species richness. Of the 24 target–neighbor habitat combinations tested, we observed three neighbor-altered habitat modifications for environmental conditions only (Figure 6; MANOVA). First, flow velocity was higher in pools (target) directly above runs (neighbor; F = 6.37; $p < 0.01$;

Figure 6a). Second, runs (target) were deeper when downstream of pools (neighbor; F = 3.07; $p < 0.1$; Figure 6b). Third, glides (target) were significantly faster upstream of riffles (neighbor; F = 6.00; $p < 0.01$; Figure 6c).

We observed three other significant neighbor–target habitat combinations that altered fish species richness within the target habitat as well as environmental variables (Figure 7; path analysis). In all three examples, species richness was *inversely* related to habitat depth. First, depth was *shallower* in riffles (target) located immediately downstream of glides (neighbor; $R^2 = 0.11$; $p < 0.05$; Figure 7a, left and middle columns), which led to an *increase* in species richness ($R^2 = 0.26$; $p < 0.05$; Figure 7a, middle and right columns). Second, riffles (target) were *deeper* when downstream of runs (neighbor; $R^2 = 0.12$; $p < 0.05$; Figure 7b, left and middle columns), which led to *lower* species richness ($R^2 = 0.31$; $p < 0.05$; Figure 7b, middle and right columns). Third, riffles (target) were significantly *shallower* and *narrower* when upstream of glides (neighbor; $R^2 = 0.16$; $p < 0.05$; Figure 7c, left and middle columns), which led to an *increase* in species richness ($R^2 = 0.26$; $p < 0.05$; Figure 7c, middle and right columns).

DISCUSSION

Understanding riverscape patterns and drivers is important for fisheries professionals (Fausch et al. 2002; Wiens 2002; Allan 2004). Managers increasingly voice their need to make science-based conservation decisions beyond a single site and time. Scaling up data from the site level to entire watersheds is difficult. We provide an approach that captures the heterogenous nature of riverine ecosystems and how the arrangement and amount of habitat influences fish diversity. Our research provided three take-home messages, reviewed in detail below that can help advance an aquatic landscape approach for fish diversity patterns in a Great Plains riverscape.

First, a gap that needs to be bridged between fisheries research and conservation are studies conducted at intermediate scales. Generally, aquatic ecologists use sampling units that are often small (stream reaches < 200 m), with data collected over disjunct locations that can, at times, span large spatial scales (e.g., watersheds). Fisheries managers, on the other hand, are often tasked with “scaling up” these data to areas that span geopolitical boundaries. Often what is missing are data collected at intermediate scales. Stream fish populations and assemblages often carry out important stages in their life history at intermediate scales (between 1–100k) and respond to changes in habitat (Fausch et al. 2002). At a small scale, habitats can be described by their type, size, shape, and location along the landscape. However, at larger scales other patterns become important including repeating patterns of small-scale heterogeneity, the presence of rare but influential features, and the role of type, size, and spatial arrangement and location. Few of these complex patterns of heterogeneity are presently described comprehensively or tested systematically in aquatic systems (or in landscape ecology metrics applied to aquatic systems), making a synthesis of larger scale heterogeneity difficult. Therefore, sampling regimes that are able to capture the composition and configuration of habitats along a riverscape, as we describe in this pilot study, provide a better understanding of aquatic landscapes that can advance solutions to persistent management problems (e.g., threatened species management, watershed restoration, sustainability, stewardship, and managing impacts such as instream barriers).

Our research identified both established and novel patterns of heterogeneity. We found stream habitats to be functionally distinct units and were delineated as pool, riffle, run, or glide based upon stream channel morphology, depth, surface flow, and sediment composition. Ecologists have long recognized that different habitat types within a local stream reach often harbor different fish communities (Taylor 2000). Treating different habitat types as separate, self-contained entities is logistically convenient and ecologically useful (Taylor 2000; Hitchman et al. 2018a). However, at a larger scale, connected habitats allowed for the quantification of various heterogeneity metrics that can go beyond simply connecting stream fishes to a particular individual habitat. For example, Hitchman et al. (2018a) found fish diversity to significantly increase with overall habitat heterogeneity in Great Plains riverscapes. Linking the distribution and arrangement of stream habitats creates mosaics across the riverscape to which heterogeneity metrics can be applied to detect underlying ecological patterns for both common and uncommon habitat types. As we have shown here, how habitats are arranged and the role of various measures of habitat heterogeneity on stream fish diversity provide important information for environmental professionals working to maintain and restore habitats at larger spatial scales.

Second, landscape ecology metrics were found to be useful in describing fish–habitat relationships in streams. We found riffle density to be a consistently important predictor of stream fish diversity. Riffles have unique ecological characteristics and can act as keystone habitats in that they disproportionately increase fish diversity across Great Plains riverscapes

(Hitchman et al. 2018a). If management goals are to conserve overall native biodiversity (at least in study systems similar to ours), then increasing the density of riffles by constructing artificial riffles may be an effective conservation strategy. Artificial riffles are used in stream restoration to increase biodiversity (Edwards et al. 1984; Favata et al. 2018) and provide habitat for threatened fish species (Fuselier and Edds 1994). To increase riffle density, artificial riffles could be constructed to meet certain minimum habitat density thresholds that increase overall habitat heterogeneity. While artificial riffles have been shown to be effective, the context of the entire mosaic of habitats needs to be considered in order to identify where and how many riffles need to be constructed to optimize management efforts. Our approach can help resource managers identify critical habitats, set minimum habitat density requirements, and apply successful spatial arrangements for restoration.

Third, the spatial arrangement of habitats (e.g., placement of habitats and the identity of neighbors) matters. While characteristics of neighboring habitats have been shown to influence species diversity in terrestrial ecosystems (Glass and Floyd 2015), examinations in aquatic ecosystems is limited. Our finding that neighbor habitats can alter characteristics of target habitats in aquatic ecosystems is novel and can explain natural variability that is especially common in lotic field studies. Target habitats often took on characteristics of flow velocity and depth found in neighboring habitats. For example, flow velocity within pools and glides increased when these were adjacent to fast-flowing habitats (e.g., riffles and runs). Relative to the effect of neighbor habitats on fish diversity, riffles were shallower when adjacent to glides, both upstream and downstream, and had increased fish diversity. Conversely, riffles were deeper when located downstream of run habitats and had decreased fish diversity. Past studies have found preferences among fish with flow-sensitive habitat types and in particular, shallow or slow flowing riffles (Gelwick 1990; Mathews 1990; Aadland 1993). These neighbor effects on fish diversity in riffle target habitats were also consistent with our within-habitat analysis, in which we found that species richness was higher in shallower, slower riffles. This demonstrates the importance of habitat arrangement along aquatic landscapes and may be considered for prescriptive solutions (e.g., placement of artificial habitats during restoration).

Our goal was to show that the type, quantity, and location of stream habitat influences fish diversity. The density of riffle habitats was an important predictor for fish diversity in low-gradient prairie streams and can be used by resource managers to plan habitat alterations that benefit watershed restoration and threatened species management. Once an understanding of how the amount and arrangement of habitats influences fish distributions and diversity, the next step would be to scale up from habitat level sampling to larger spatial extents. While our primary focus was on maintaining native fish diversity, this approach could potentially be used for other important metrics (e.g., abundance, functional guilds). For example, if conservation of a threatened or endangered species is a priority, our methods could be adapted to identify critical habitat and the influence neighboring habitats have on the abundance of the species of concern. Furthermore, managers could prescribe minimum habitat density requirements that could be evaluated using emerging technology (e.g., geographic information systems, drones). Our approach can be used to identify similar critical habitats in other systems and to explore how habitat arrangement may influence other ecological processes (e.g., trophic food webs, energy flow, predator–prey dynamics).

ACKNOWLEDGMENTS

The project was funded by a State Wildlife Grant provided by the United States Fish and Wildlife Service and the Kansas Department of Wildlife, Parks, and Tourism, and administered through the Kansas Cooperative Fish and Wildlife Research Unit (Kansas State University, the U.S. Geological Survey, U.S. Fish and Wildlife Service, the Kansas Department of Wildlife, Parks, and Tourism, and the Wildlife Management Institute). The research presented above was conducted under the auspices of Kansas State University IACUC Protocol #3170. We are grateful to numerous private landowners for granting access to the Neosho and Cottonwood rivers. Many colleagues including J. Fencl, E. Johnson, J. Luginbill, M. Daniels, W. Dodds, A. Joern, and J. Hofmeier provided helpful feedback throughout the conceptualization and implementation of this project. S. Chatterjee, C. Pennock, J. Danner, K. McCullough, and C. Lee provided field assistance. D. Ostendorf, and R. Hrabik provided advice and assistance on sampling gear and fish ecology. M. Henderson and two anonymous reviewers provided useful feedback. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. government.

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Table 1. Multiple regression models that examine relationships between species richness (response) and landscape metrics (predictor) such as habitat size, habitat shape, habitat density for all four habitat types. Bolded denotes significant standardized β (slopes) at α = 0.05 and () displays standard errors. df = degrees of freedom. The model average and variable importance are listed at the base of the table. Model averaged β was calculated as the mean slope for each predictor across models. Variable importance was calculated as the proportion of candidate models for which each predictor was included.

Riffle density (ß)	% Variation Explained	**Riffle area (ß)**	% Variation Explained	**Glide area (ß)**	% Variation Explained	**Riffle Perimeter–area ratio (ß)**	% Variation Explained	**Run area (ß)**	% Variation Explained	Model R2	*p*	AICc	Delta	Weight
3.2 **(0.6)**	76.64	**2.0** **(0.6)**	23.36							0.80	0.00	53.20	-	0.30
2.2 **(0.7)**	54.32			**1.9** **(0.7)**	45.68					0.70	0.00	53.70	0.40	0.20
3.3 **(0.7)**	80.27					**-1.9** **(0.7)**	19.73			0.70	0.01	54.30	1.10	0.20
4.0 **(0.9)**	84.75							**2.2** **(0.9)**	15.25	0.70	0.01	55.10	1.90	0.10

Model Average									
3.1		2.0		1.9		-1.91		2.2	
(0.7)	74.00	(0.6)	23.36	(0.7)	45.68	(0.69)	19.73	(0.9)	15.25
1.00		0.25		0.25		0.25		0.25	

Figure Captions

Figure 1. Conceptual diagram outlining (I) types of larger scale heterogeneity and (II) our specific research questions related to larger-scale heterogeneity and fish biodiversity.

Figure 2. Map of study area representing ten 3-km study sites located along the Neosho and Cottonwood rivers, Kansas. Black dots represent low-head dam sites and gray dots undammed sections of the rivers. The city of Emporia is represented by a star. Note: habitat–fish diversity relationships are not explained by the presence of low-head dams.

Figure 3. Non-metric multidimensional scaling (NMDS) biplot (Stress = 0.03) for stream habitats at ten 3-km study sites located along the Neosho and Cottonwood rivers, Kansas. Points represent each habitat sample *(N* = 138). Colored ellipses indicate 95% standard error confidence ellipses for the mean. Analysis of similarity indicates significant separation among each habitat type (ANOSIM Global R = 0.30, *p* = 0.001).

Figure 4. Longitudinal profiles for each of ten 3-km study sites along the Neosho and Cottonwood rivers, Kansas. Represented are mean habitat area, total number of habitats (N), and overall habitat diversity calculated using Shannon's Diversity Index (H'). Habitat types are shown in different colors.

Figure 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.

Figure 6. Boxplots showing significant relationships of within habitat characteristics relative to neighbor (adjacent) habitats: (a) illustrates how flow velocity within pool habitats is influenced by downstream neighbor habitats, (b) illustrates how depth within run habitats is influenced by upstream neighbor habitats, and (c) illustrates how flow velocity within glide habitats is influenced by downstream neighbor habitats. The box represents the second and third quartiles, whiskers show the first and fourth quartiles, and heavy horizontal lines depict the median.

Figure 7. Path analyses investigating direct and indirect relationships for species richness within (a) riffle habitats that were located immediately downstream of glides, (b) riffle habitats that were located immediately downstream of runs, and (c) riffle habitats that were located immediately upstream of glides. We only show significant relationships at $\alpha = 0.05$. 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).

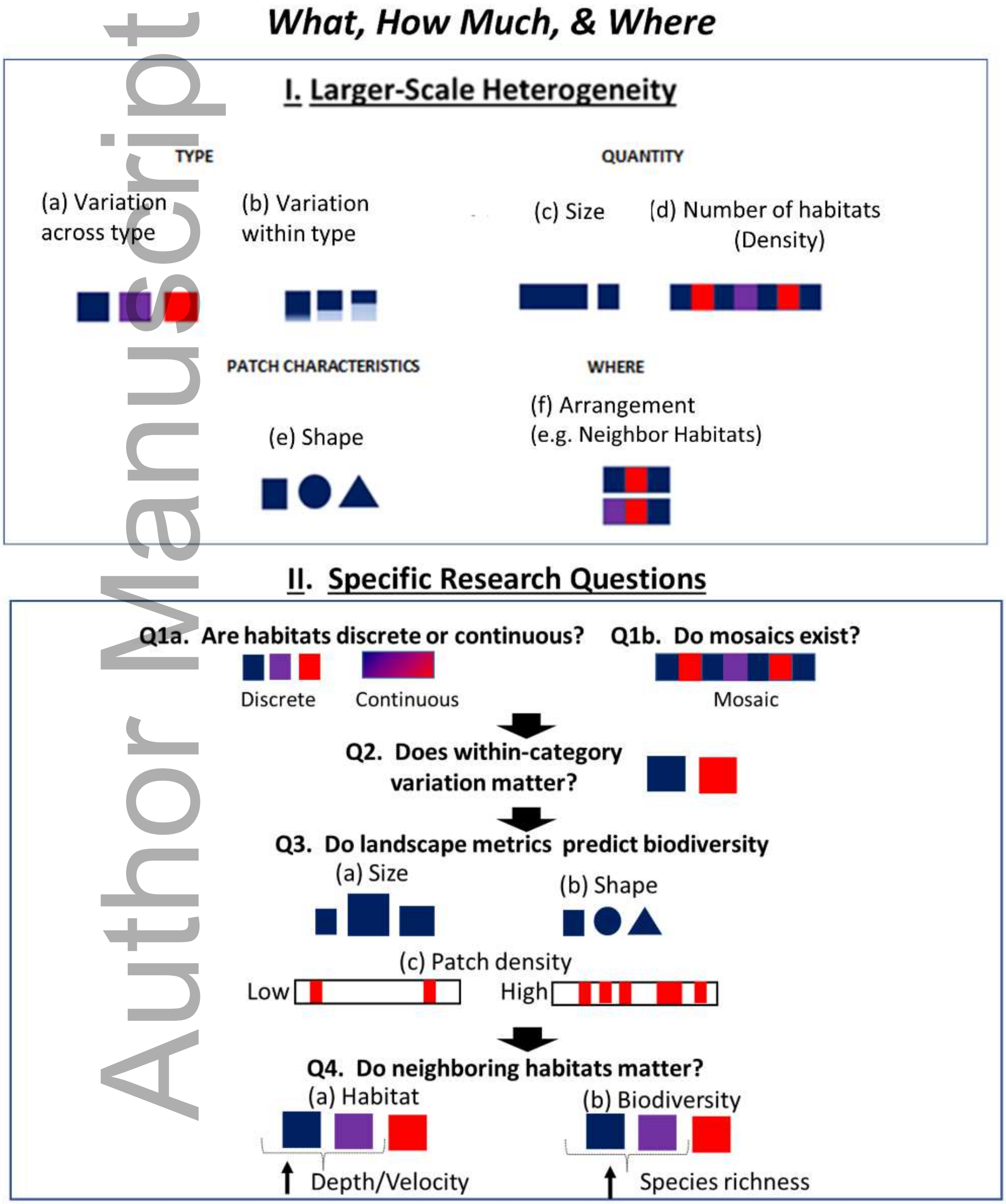
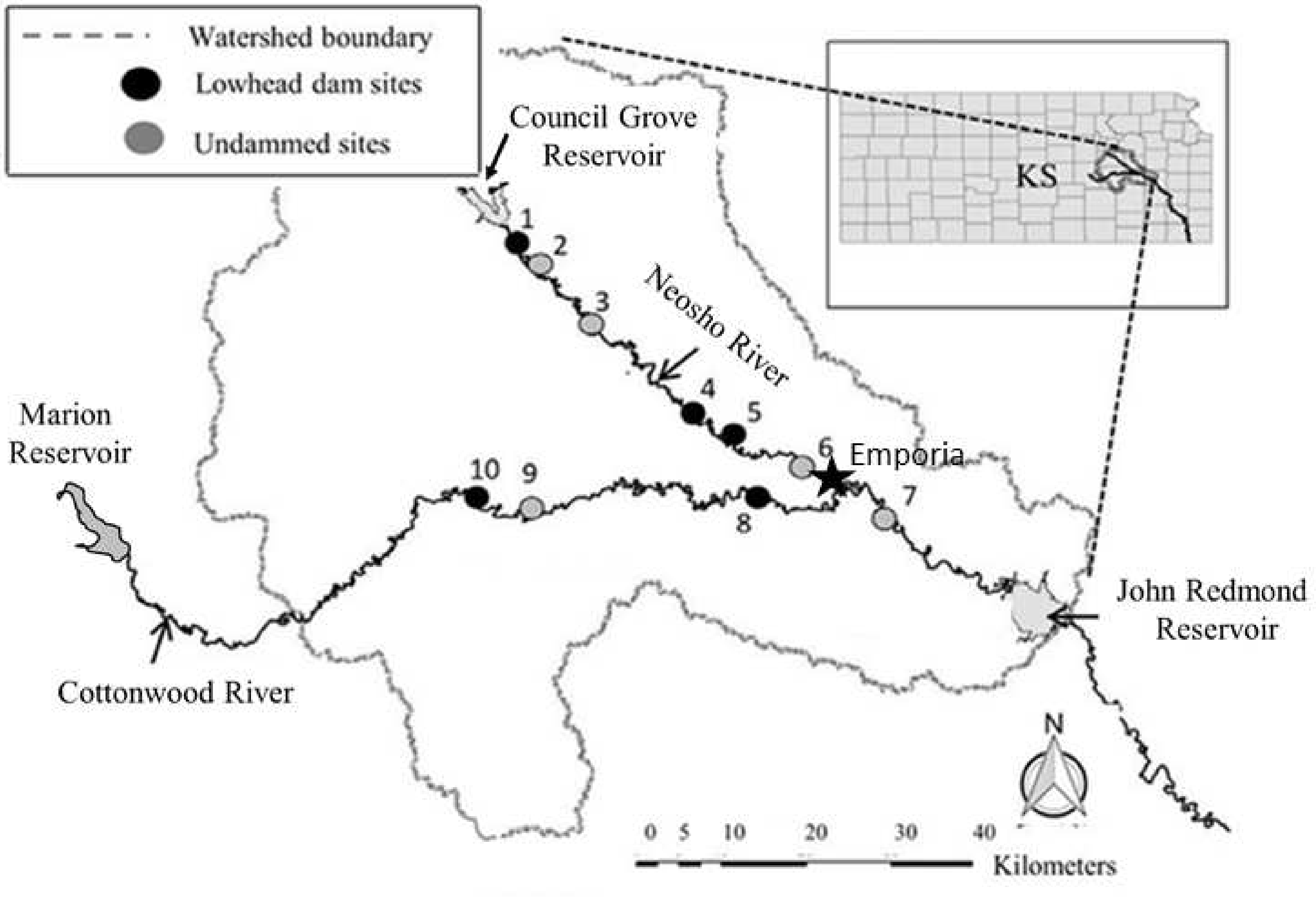

What, How Much, & Where
I. Larger-Scale Heterogeneity
TYPE
(a) Variation across type
(b) Variation within type
QUANTITY
(c) Size
(d) Number of habitats (Density)
PATCH CHARACTERISTICS
(e) Shape
WHERE
(f) Arrangement (e.g. Neighbor Habitats)
II. Specific Research Questions
Q1a. Are habitats discrete or continuous?
Discrete
Continuous
Q1b. Do mosaics exist?
Mosaic
Q2. Does within-category variation matter?
Q3. Do landscape metrics predict biodiversity
(a) Size
(b) Shape
(c) Patch density
Low
High
Q4. Do neighboring habitats matter?
(a) Habitat
Depth/Velocity
(b) Biodiversity
Species richness

Figure 1



Watershed boundary
Lowhead dam sites
Undammed sites
Council Grove Reservoir
KS
1
2
3
4
5
6
7
8
9
10
Neosho River
Emporia
Marion Reservoir
Cottonwood River
John Redmond Reservoir
N
0 5 10 20 30 40
Kilometers

Figure 2

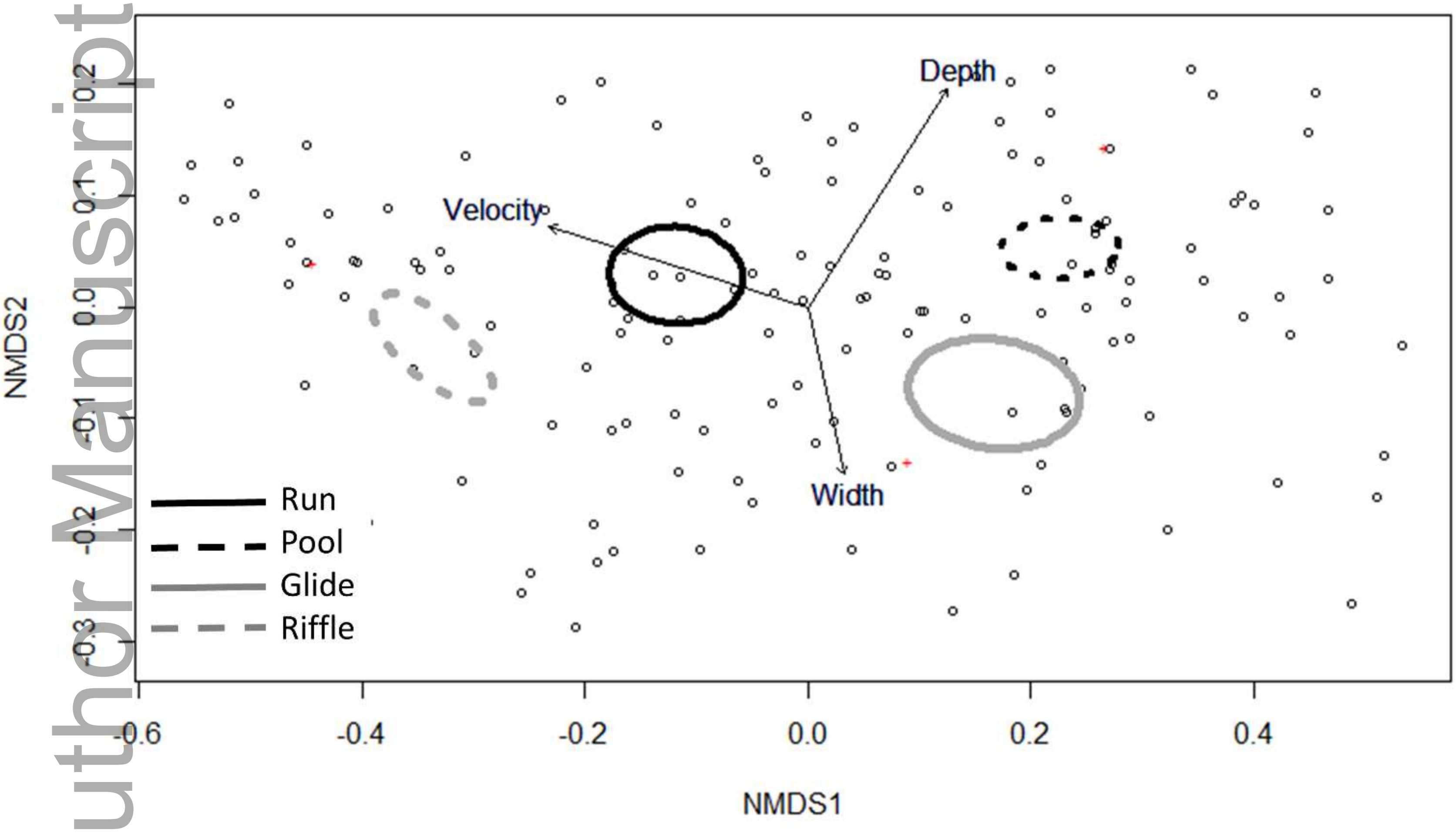

Depth
Velocity
Width
Run
Pool
Glide
Riffle
NMDS2
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.6
-0.4
-0.2
0.0
0.2
0.4
NMDS1

Figure 3

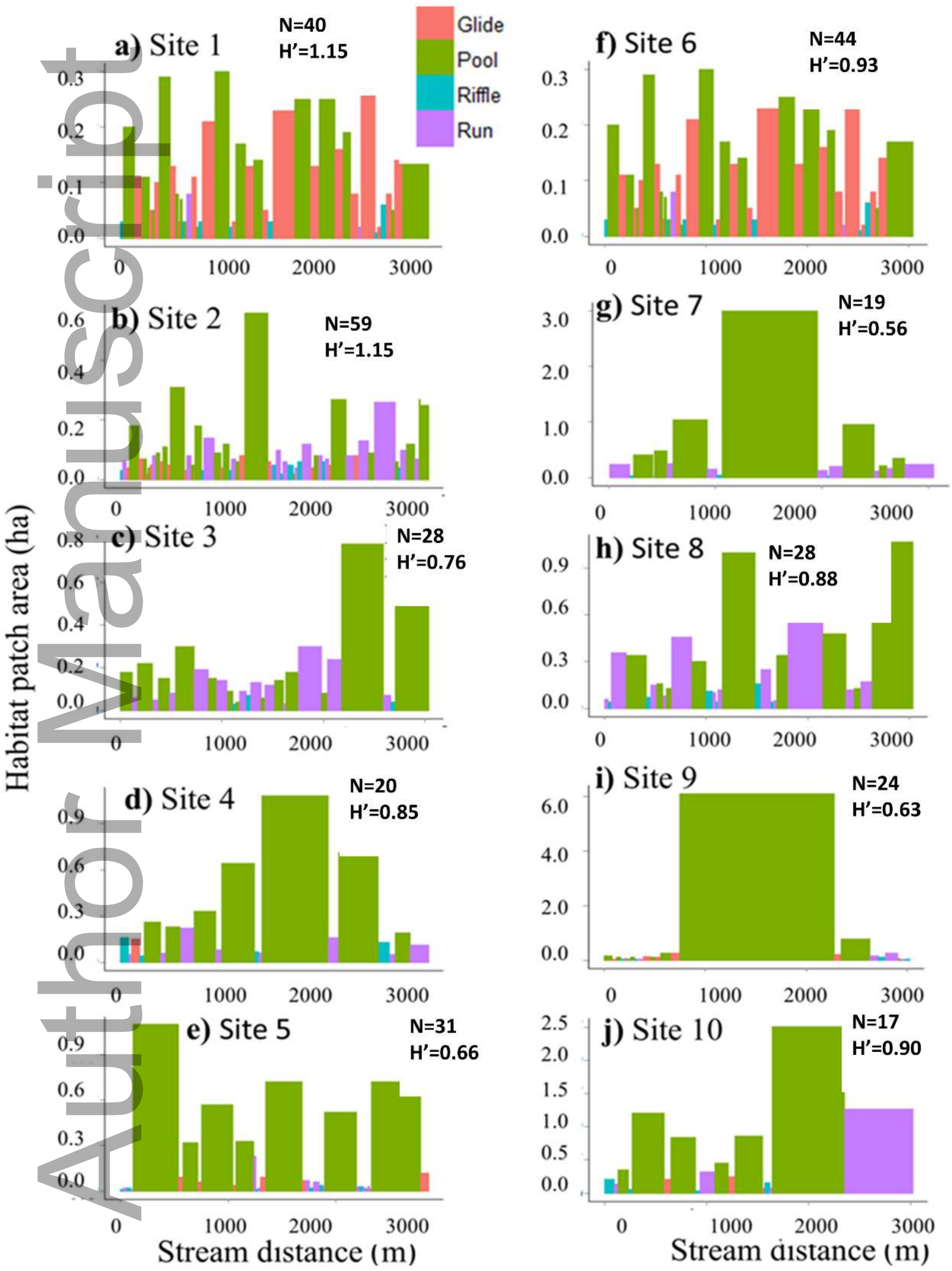

a) Site 1
N=40
H'=1.15
Glide
Pool
Riffle
Run
f) Site 6
N=44
H'=0.93
b) Site 2
N=59
H'=1.15
g) Site 7
N=19
H'=0.56
c) Site 3
N=28
H'=0.76
h) Site 8
N=28
H'=0.88
d) Site 4
N=20
H'=0.85
i) Site 9
N=24
H'=0.63
e) Site 5
N=31
H'=0.66
j) Site 10
N=17
H'=0.90
Habitat patch area (ha)
Stream distance (m)
Stream distance (m)
0
1000
2000
3000

Figure 4

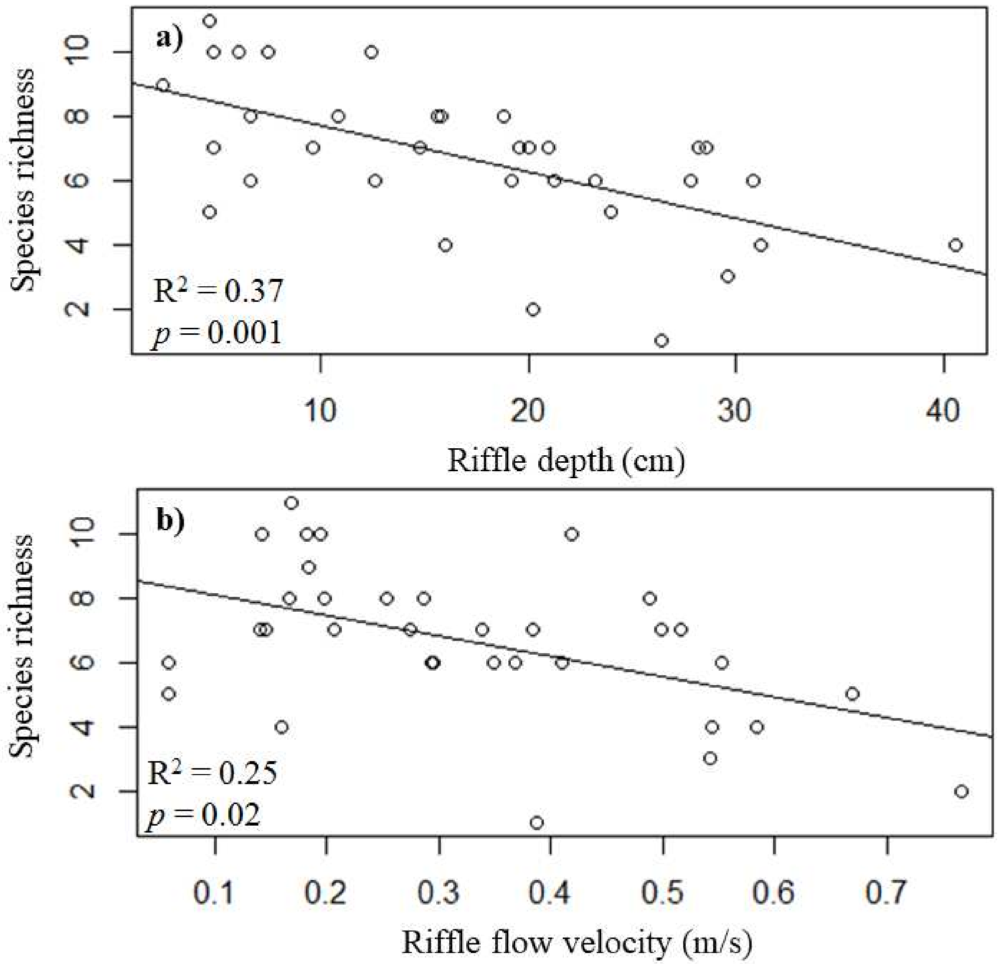

a)
Species richness
2
4
6
8
10
R² = 0.37
p = 0.001
10
20
30
40
Riffle depth (cm)
b)
Species richness
2
4
6
8
10
R² = 0.25
p = 0.02
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Riffle flow velocity (m/s)

Figure 5

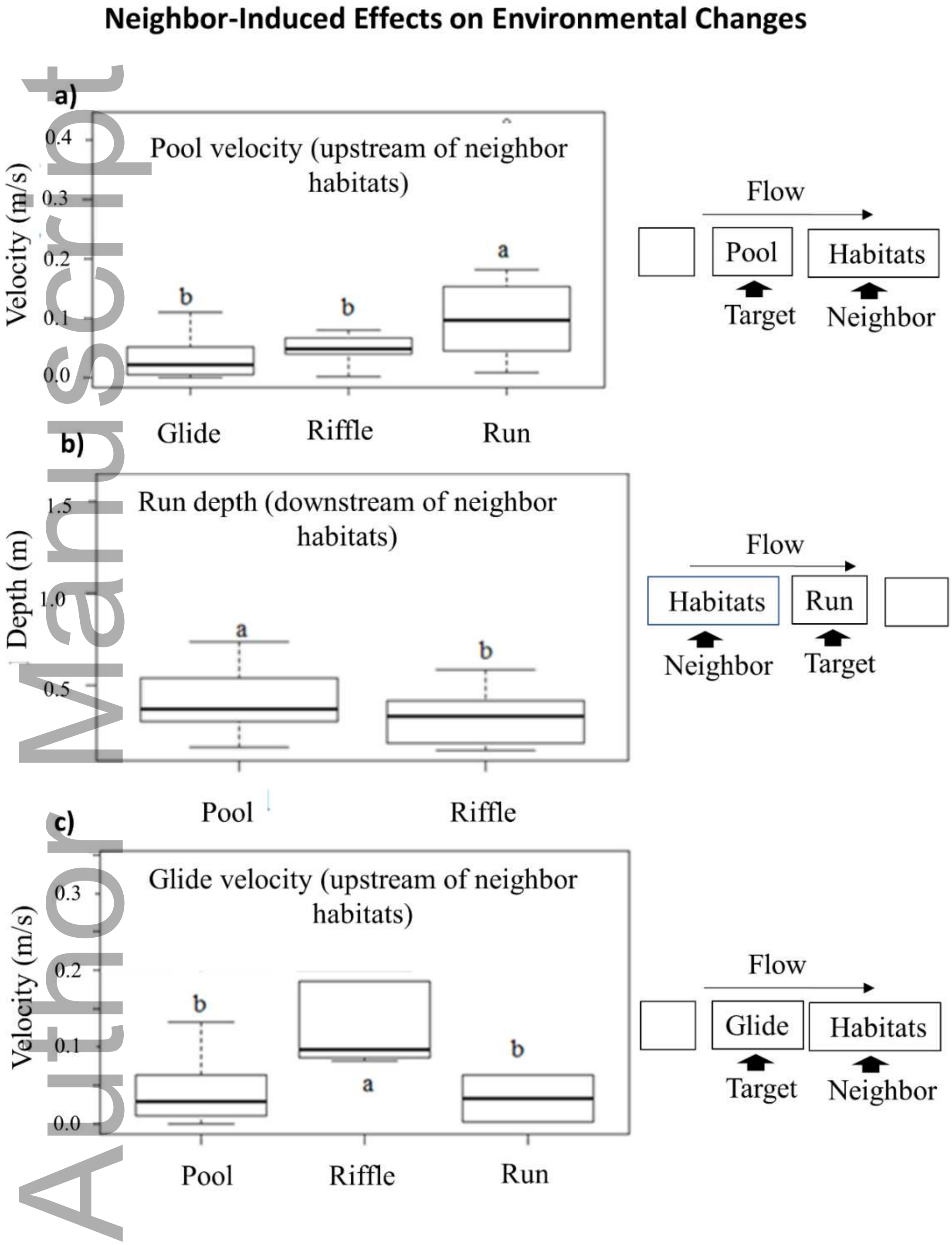

Neighbor-Induced Effects on Environmental Changes
a)
Pool velocity (upstream of neighbor habitats)
Velocity (m/s)
0.4
0.3
0.2
0.1
0.0
b
b
a
Glide
Riffle
Run
Flow
Pool
Habitats
Target
Neighbor
b)
Run depth (downstream of neighbor habitats)
Depth (m)
1.5
1.0
0.5
a
b
Pool
Riffle
Flow
Habitats
Run
Neighbor
Target
c)
Glide velocity (upstream of neighbor habitats)
Velocity (m/s)
0.3
0.2
0.1
0.0
b
a
b
Pool
Riffle
Run
Flow
Glide
Habitats
Target
Neighbor

Figure 6

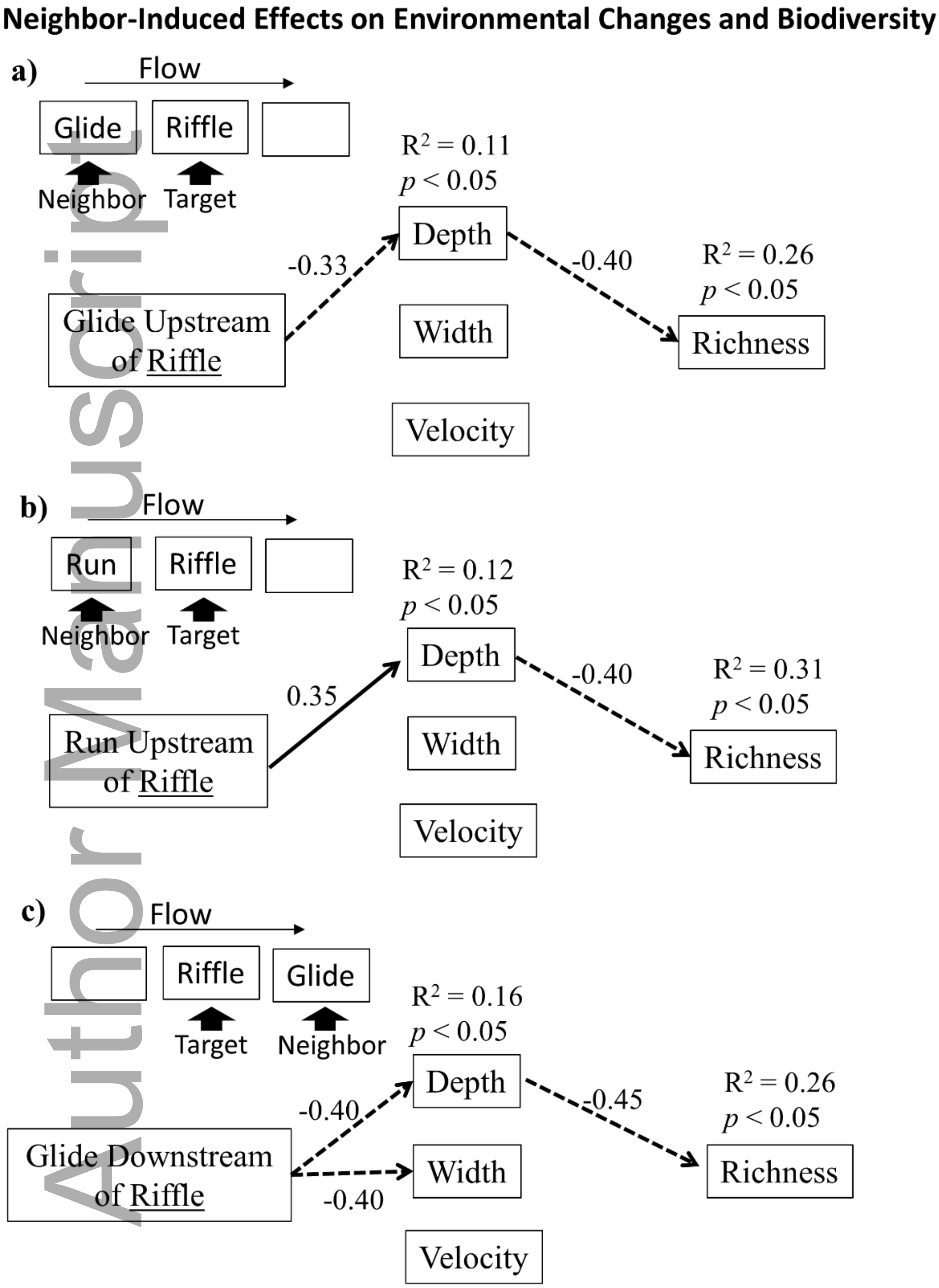

Neighbor-Induced Effects on Environmental Changes and Biodiversity
a)
Flow
Glide
Riffle
Neighbor
Target
R² = 0.11
p < 0.05
Depth
-0.33
-0.40
R² = 0.26
p < 0.05
Glide Upstream of Riffle
Width
Richness
Velocity
b)
Flow
Run
Riffle
Neighbor
Target
R² = 0.12
p < 0.05
Depth
-0.40
R² = 0.31
p < 0.05
0.35
Run Upstream of Riffle
Width
Richness
Velocity
c)
Flow
Riffle
Glide
Target
Neighbor
R² = 0.16
p < 0.05
Depth
-0.45
R² = 0.26
p < 0.05
-0.40
Glide Downstream of Riffle
Width
Richness
-0.40
Velocity

Figure 7