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Habitat mosaics and path analysis can improve biological conservation of aquatic biodiversity in ecosystems with low-head dams

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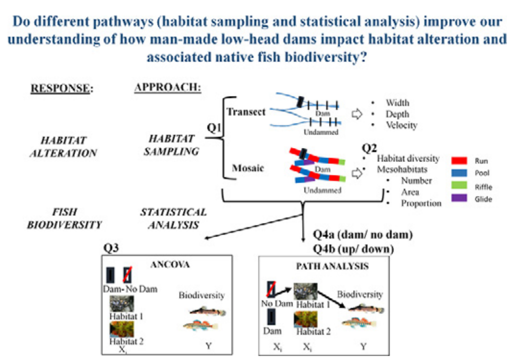
HIGHLIGHTS

- Low-head dams are ubiquitous impacts that represent a challenge for environmental management worldwide.
- Our research quantifies how low-head dams affect habitat and biodiversity in lotic ecosystems.
- Continuous sampling of habitat mosaics revealed new insights into stream fish-habitat relationships.
- Both direct and mediated effects of habitat on biodiversity should be considered when outlining management strategies.
- Here, we provide science-based guidance for environmental practitioners who must manage aquatic systems with dams.

GRAPHICAL ABSTRACT



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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

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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.

1. 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). 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. 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

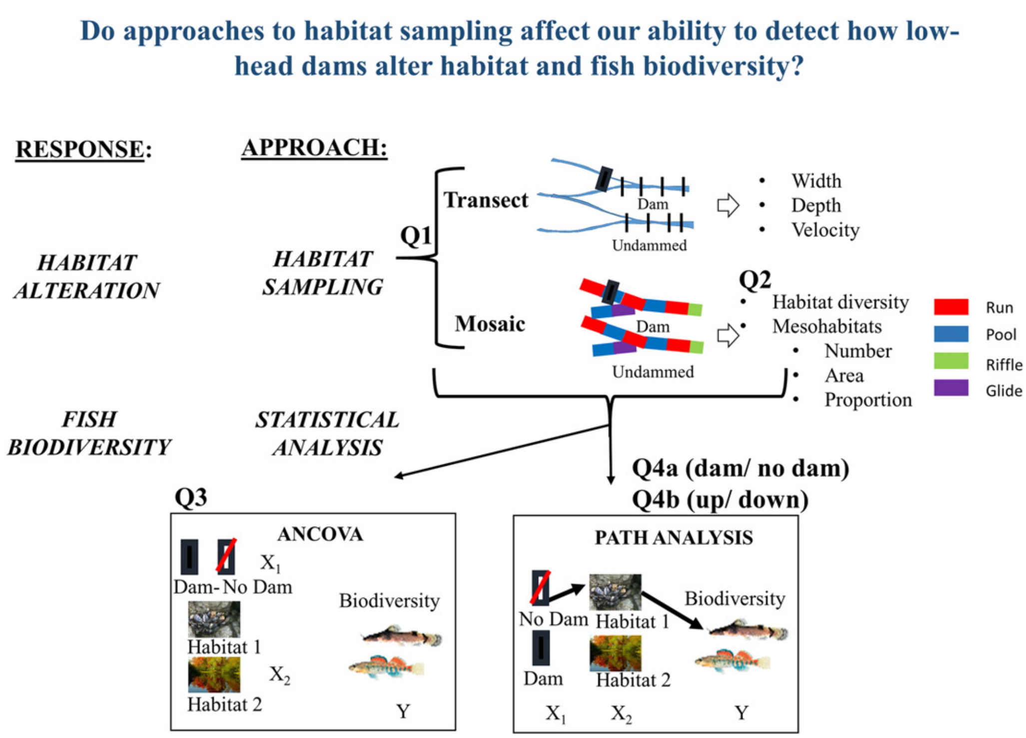

Fig. 1. Conceptual diagram illustrating how our research tests alternate approaches to habitat sampling and statistical analyses, which can alter stream habitat and fish biodiversity. Our four specific research questions are indicated.

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 et al., 2017). 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 nonmetric 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. 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.

2. Materials and methods

2.1. 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 7770 km^2 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 km^2 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 m^3/s, Neosho River, USGS gage 07179730; 13.0–19.0 m^3/s Cottonwood River, USGS gage 07182250) were similar at the time of sampling.

2.2. General sampling regime

Sampling occurred during baseflow conditions at five low-head dam sites and at five undammed sites (Fig. 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. 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 these low-head dams are <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). Site 7 was located just below the confluence of the Neosho and Cottonwood Rivers (Fig. 2). Three sites (8–10) were located on the Cottonwood River (Fig. 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. 3).

2.3. Specific sampling and analyses

2.3.1. 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 1).

2.3.2. 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

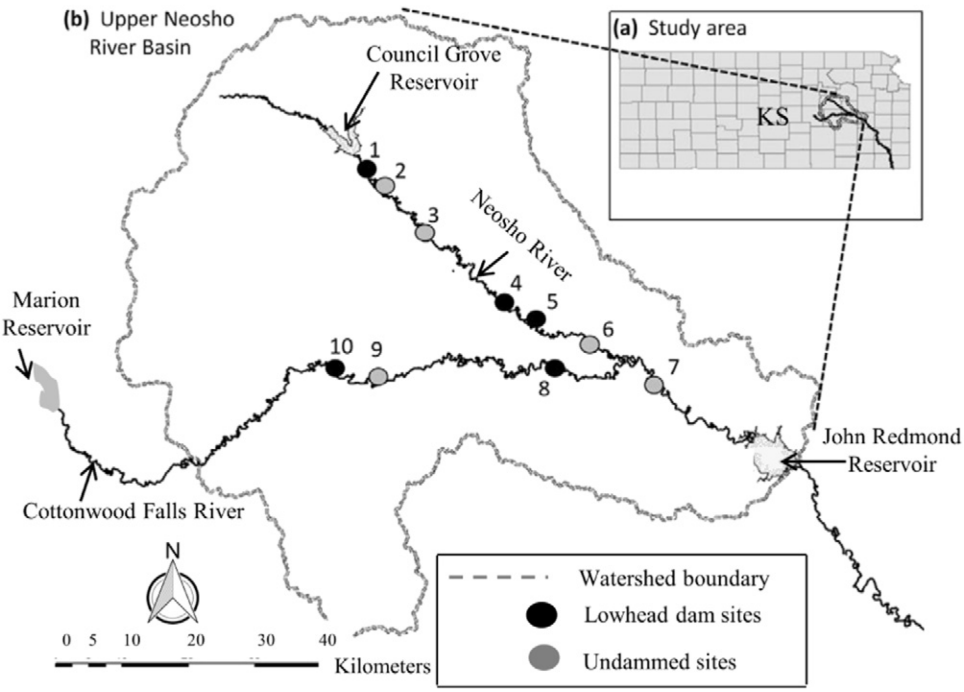

Fig. 2. Map of study area including (a) Neosho River within the state of Kansas, and (b) 10 3-km sampling sites within the Upper Neosho River basin along the Neosho and Cottonwood Rivers, KS, below five low-head dam sites and at five undammed sites.

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.

2.3.3. 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 1). In this study, patches equate to individual mesohabitats, classes represent each mesohabitat type, and landscape corresponds to each of our ten sample sites.

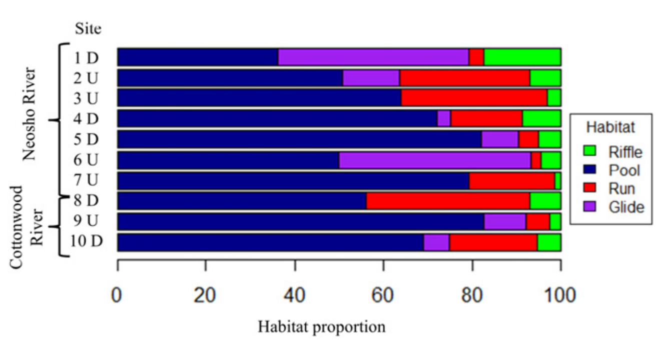

Fig. 3. Horizontal stacked bar plot of the relative proportion of mesohabitats (riffle, pool, run, glide) at five dammed (D) and five undammed (U) sites along the Neosho and Cottonwood Rivers, KS. Sample sites are numbered as shown in Fig. 2.

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.

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

Table 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

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

2.3.6. 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).

2.3.7. Transect vs. mosaic habitat at dammed and undammed sites; ANCOVA on fish biodiversity (Q3; Fig. 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.

2.3.8. Transect vs. mosaic habitat at dammed and undammed sites; path analysis on fish biodiversity (Q4a; Fig. 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).

2.3.9. Transect vs. mosaic habitat upstream and downstream of dams; path analysis on fish biodiversity (Q4b; Fig. 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/h 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 (Core Development Team, 2013). Throughout we report p values and clearly state comparisons made (Wasserstein and 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).

3. Results

3.1. Transect vs. mosaic habitat data (Q1)

3.1.1. Habitat transect approach

Differences in means of habitat transect variables were relatively small downstream of dams compared to undammed sites (Fig. 4a–c). *Width* was the only habitat transect variable that was significantly different ($W = 2261$, $p < 0.001$; Fig. 4a). Specifically *width* was greater below dams than at undammed sites. The other two habitat transect variables, *depth* ($W = 1677$, $p = 0.69$; Fig. 4b) and *velocity* ($W =$

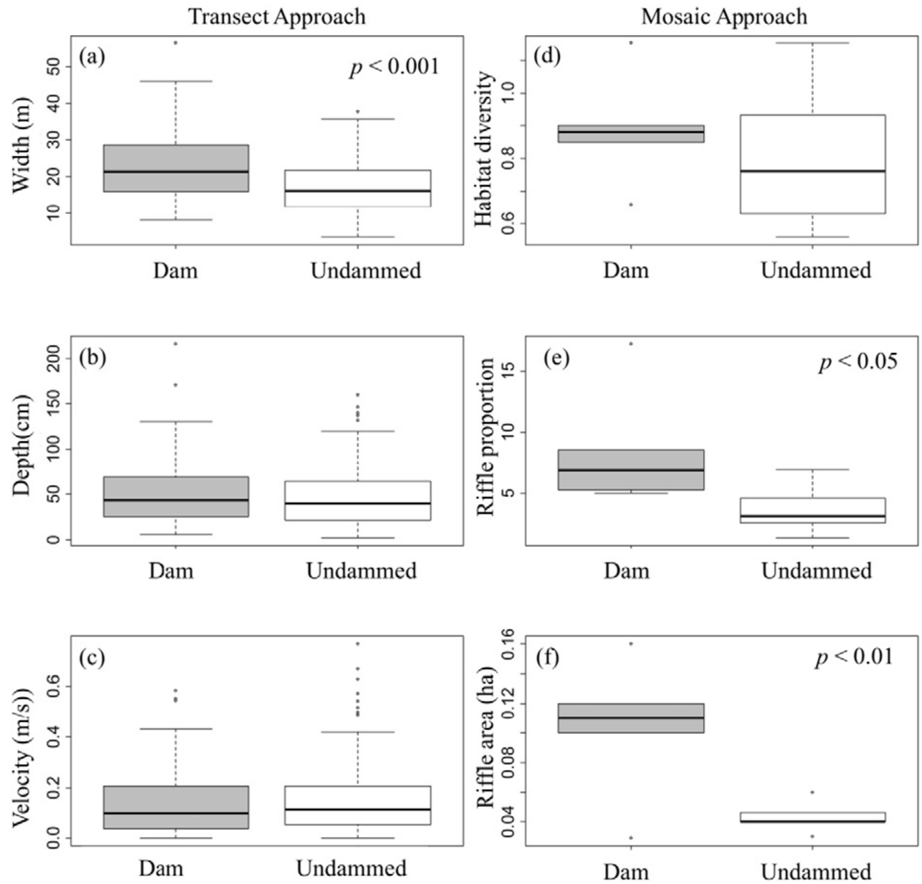

Fig. 4. Boxplots showing six habitat variables (a–f) at dammed (downstream) and undammed sampling sites. Habitat data were collected using both (a–c) transect and (e–f) mosaic approaches. *P* values are presented for significant relationships. Data are represented by a boxplot in which the heavy horizontal line depicts the median, the box represents the 2nd and 3rd quartiles, and the whiskers show the 1st and 4th quartiles.

1552, $p = 0.76$; Fig. 4c), were not significantly different between dammed and undammed sites.

3.1.2. 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. 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. 4d), the *proportion of riffle* ($W = 25$, $p < 0.05$; Fig. 4e) and *area of riffle habitat* ($W = 684$, $p < 0.01$; Fig. 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.

3.2. Low-head dam effects on habitat variability (Q2)

Although mean *habitat diversity* did not differ (Fig. 4d), dammed sites had less variation in stream *habitat diversity* than undammed sites (Fig. 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 ($\chi^2 = 50.57$, $p < 0.001$), such that low-head dams depressed natural variability in habitat.

3.3. Transect vs. mosaic habitat; fish biodiversity (Q3)

We captured a total of 8033 fish representing 36 species encompassing 18 genera upstream and downstream of five low-head dam sites and five undammed sites along the UNRB (Table A.1). 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. 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. 6a], *depth* [habitat ($F = 0.25$; df = 3, 6; $p = 0.64$); dam treatment ($F = 0.60$; df = 3, 6; $p = 0.47$); Fig. 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. 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. 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. 6d], and *proportion of riffle habitat* [habitat ($F = 10.92$; df = 3,

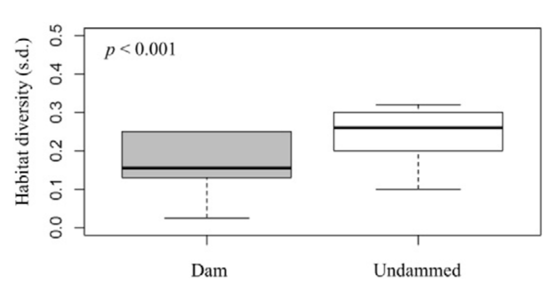

Fig. 5. Comparison of standard deviation in habitat diversity at dammed (downstream) and undammed sites. Data are the result of a bootstrapping procedure designed to quantify variation in habitat diversity. Data are represented by a boxplot in which the heavy horizontal line depicts the median, the box represents the 2nd and 3rd quartiles, and the whiskers show the 1st and 4th quartiles.

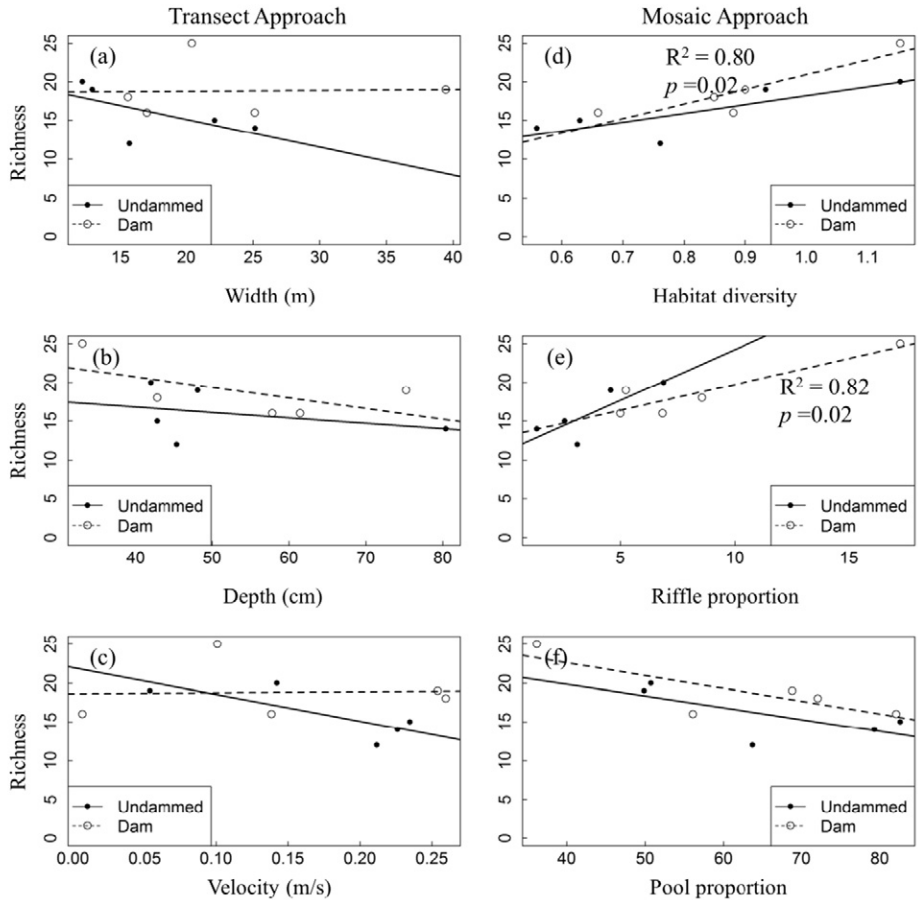

Fig. 6. Regression plots depicting results of an ANCOVA analysis examining the relationship between species richness and habitat at dammed (downstream) and undammed sites. Habitat data were collected using (a–c) transect and (e–f) mosaic approaches. R^2 and *p* values are presented for significant relationships.

6; $p = 0.02$); dam treatment ($F = 0.48$; df = 3, 6; $p = 0.52$); Fig. 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. 6f].

3.4. Transect vs. mosaic habitat at dammed and undammed sites; path analysis on fish biodiversity (Q4a, Fig. 1)

3.4.1. Habitat transect data - below dams

No significant, mediated effects of low-head dams on fish species richness were detected using habitat transect data (Fig. 7a). 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. 7a; middle and right columns). *Depth* and *velocity* were inversely proportional to species richness ($R^2 = 0.07$; $p < 0.05$; Fig. 7a, middle and right columns), but were not significantly different between dammed and undammed sites (Fig. 7a; left and middle columns).

3.4.2. 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. 7b). Sites below low-head dams had significantly higher *proportions of riffle* habitat ($R^2 = 0.33$; $p < 0.03$, Fig. 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. 7b, middle and right columns). *Habitat diversity* and *proportion of pool* were related to species richness (Fig. 7b, middle and right columns), but were not consistently different between dammed and undammed sites (Fig. 7b, left and middle columns).

3.5. Transect vs. mosaic habitat upstream and downstream of dams; path analysis on fish biodiversity (Q4b, Fig. 1)

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. 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. 7-'IKc; top arrows left, middle, right columns).

3.6. Basin-wide dam impacts

Downstream dam-impacts on habitat were substantial (Fig. 8 – red lines), but the geographic extent of upstream low-head dam impacts on habitat was even greater (Fig. 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. 8).

4. 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

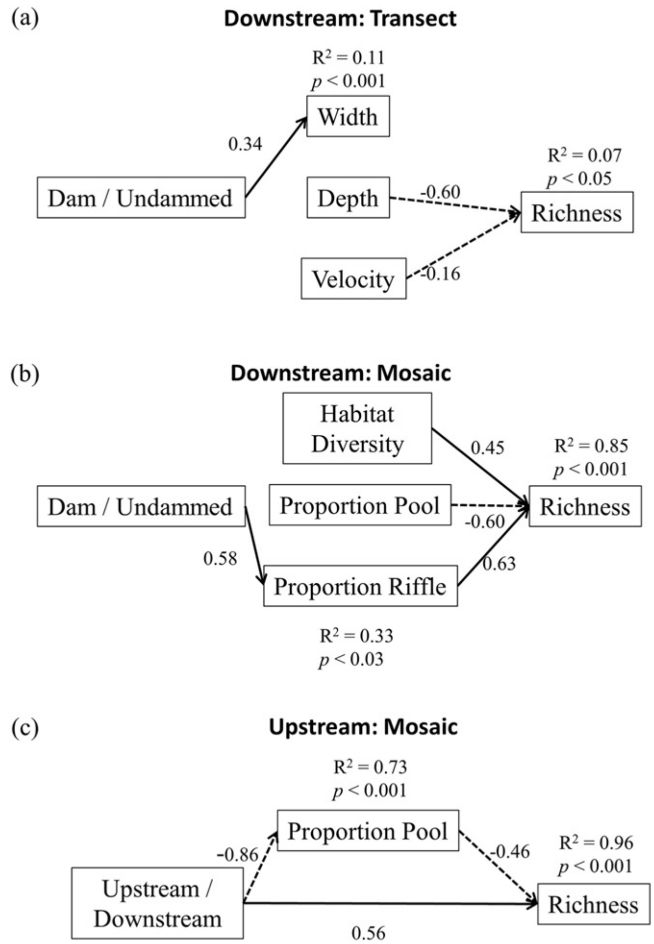

Fig. 7. Path analyses for species richness at (a) dammed (downstream) versus undammed locations using habitat transect data, (b) dammed (downstream) versus undammed locations using habitat-mosaic data and (c) the upstream vs. downstream effects of low-head dams using habitat mosaic data. Due to high collinearity, proportion of pool habitat was the only variable used in the upstream-downstream model. We only show significant relationships at $\alpha = 0.05$. 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).

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 et al., 2017). 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 that 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 diversity* (Figs. 4, 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).

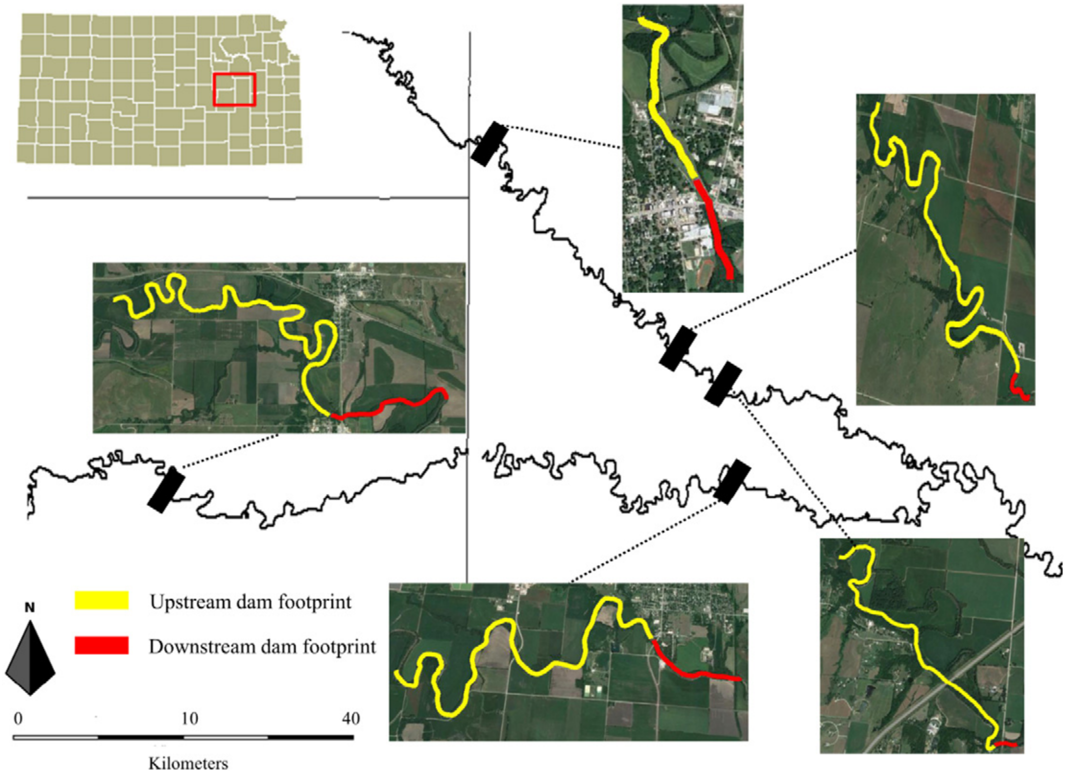

Fig. 8. Map showing upstream (yellow tracks) and downstream (red tracks) geomorphic dam footprints at five low-head dams in the Upper Neosho River basin. The five inserts represent our five dam study sites. The maps indicate upstream and downstream dam footprints which comprise a substantial component (17%) of the Upper Neosho River basin.

The path analysis integrated discrepancies among individual analyses by showing that *habitat diversity*, *proportion of riffle*, *proportion 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.

5. Conclusions

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.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2017.10.272.

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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. EPA 841-B-99-002, second edition 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. Biol. Conserv. 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 Interdiscip. Rev. Water 4. https://doi.org/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. Ecol. Appl. 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. Glob. Chang. Biol. https://doi.org/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. Sci. Total Environ. 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 Res. Appl. 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. Environ. Biol. Fish 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. Sci. Total Environ. 586, 879–889.

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

Csiki, S.R., Rhoads, B.L., 2010. Hydraulic and geomorphological effects of run-of-river dams. Prog. Phys. Geogr. 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. J. Great Lakes Res. 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. Ecol. Freshw. 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. https://doi.org/10.1371/journal.pone.0141210.

Fencl, J.S., Mather, M.E., Smith, J.M., Hitchman, S.M., 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). https://doi.org/10.1002/ecs2.1973.

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. Water Science and Technology Board, National Research Council. Sustaining our Water Resource. National Academy Press, Washington, D.C, 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. Ecol. Appl. 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 Res. Appl. 25, 160–180.

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. American Journal of Fisheries Management.]–>N. Am. J. Fish Manag. 36, 1358–1367.

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

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. Regul. Rivers Res. Manag. 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. American Benthological Society.]–>J. N. Am. Benthol. Soc. 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. J. Freshw. Ecol. 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. Glob. Chang. Biol. 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.]–>N. Z. J. Mar. Freshw. Res. 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 Jr., N.H., 2013. A fish index of biotic integrity for South Dakota's northern glaciated plains ecoregion. Ecol. Indic. 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. Zool. Res. 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. American Journal of Fisheries Management.]–>N. Am. J. Fish Manag. 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. Compt. Rendus Geosci. 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. Landsc. Ecol. 15, 563–576.

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

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.

Poulet, N., 2007. Impact of weirs on fish communities in a piedmont stream. River Res. Appl. 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. American Benthological Society.]–>J. N. Am. Benthol. Soc. 7, 503–524.

Puckridge, J.T., Sheldon, F., Walker, K.F., Boulton, A.J., 1998. Flow variability and the ecology of large rivers. Mar. Freshw. Res. 49, 55–72.

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

Rahel, F.J., 2007. Biogeographic barriers, connectivity, and biotic homogenization: it's a small world after all. Freshw. Biol. 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. American Journal of Fisheries Management.]–>N. Am. J. Fish Manag. 25, 1353–1366.

Rosseel, Y., 2012. Lavaan: an R package for structural equation modeling. J. Stat. Softw. 48, 1–36.

Rowe, D.C., Pierce, C.L., Wilton, T.F., 2009. Fish assemblage relationships with physical habitat in wadeable Iowa streams. N. Am. J. Fish Manag. 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. Mar. Biol. 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. American Journal of Fisheries Management.]–>N. Am. J. Fish Manag. 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. American Journal of Fisheries Management.]–>N. Am. J. Fish Manag. 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. American Journal of Fisheries Management.]–>N. Am. J. Fish Manag. 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. Freshw. Biol. 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. Ecol. Appl. 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 Resour. Res. 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. American Fisheries Society.]–>Trans. Am. Fish. Soc. 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. Biol. Conserv. 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. American Water Resources Association.]–>J. Am. Water Resour. Assoc. 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. American Statistician.]–>Am. Stat. 70, 129–133.
Watters, G.T., 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoidia) and their hosts. Biol. Conserv. 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. American Journal of Fisheries Management.]–>N. Am. J. Fish Manag. 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. Freshw. Biol. 47, 501–515.
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. Environ. Biol. Fish 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.

Table A.1: Abundances of fish species collected along the Neosho and Cottonwood Rivers, KS June-August, 2013.

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