

Accounting for dispersal and local habitat when evaluating tributary use by riverine fishes

COREY G. DUNN ^{1,3,†} AND CRAIG P. PAUKERT ^{1,2}

¹Missouri Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, Missouri 65211 USA

²U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, Missouri 65211 USA

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Abstract. Conservation practitioners increasingly recognize the conservation value of tributaries for supporting mainstem, large-river specialist fishes. A tributary's discharge at its mouth is a coarse indicator of the richness of large-river specialists found within the tributary, but the relative influences of regional dispersal and local habitat underpinning this species–discharge relationship are often unknown. We sampled large-river specialist fishes at sites within two nonwadeable tributaries of the Missouri and Mississippi rivers with contrasting prairie (Grand River) vs. upland (Meramec River) habitats to address four research questions: (1) Do alpha diversity (mean site-level species richness) and beta diversity (among-site species compositional differences) vary between tributaries? (2) Does mean annual discharge correlate with local habitat and downstream distance to mainstem rivers (i.e., mainstem connectivity)? (3) Are slopes of species–discharge relationships consistent between tributaries? And (4) Do local habitat and downstream distance explain residual richness at sites beyond variation already explained by species–discharge relationships? We detected 30 of 42 potential large-river specialist fishes, demonstrating most mainstem species use tributaries. Mean site richness was higher in the Grand River (12.5 species vs. 9.8 species in Meramec River), but partitioning of lower reaches (sites < 116 km from river mouth) and dispersal limitation in upper reaches (sites ≥ 145 km from river mouth) caused Meramec River beta diversity to be three times higher. Mean annual discharge correlated with habitat availability at sites and downstream distance to a mainstem. Although site-level alpha richness generally increased with discharge in both tributaries, slopes of species–discharge relationships varied between tributaries. Analyzing species–discharge residuals revealed downstream distance explained additional variation in site-level richness not accounted for by local discharge. For example, discharge alone underrepresented richness in lower-discharge sites accessible to dispersers (maximum underestimate = 8.7 species) and overrepresented richness in isolated sites (maximum overestimate = 5.8 species). Thus, predictive performance of species–discharge relationships can be improved by accounting for varying habitats among tributaries and downstream distance of sites to mainstems when valuing tributaries for fishes with dispersal-dependent life cycles.

Key words: Alabama Shad; beta diversity; connectivity; flow–ecology relationship; large river; nestedness; richness; spatial turnover; species–discharge relationship.

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³Present address: U.S. Geological Survey, Mississippi Cooperative Fish and Wildlife Research Unit, Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State Mississippi 39762 USA.

† E-mail: cdunn@usgs.gov

INTRODUCTION

Large rivers support unique fish assemblages comprised of species adapted for seasonally predictable, expansive, and open riverine ecosystems (Winemiller 2005). However, few free-flowing mainstem rivers remain in industrialized countries (Grill et al. 2019), and habitats in many of these rivers are compromised by dredging, channelization, and flow regulation causing declines in many large-river fishes and fisheries (Rinne et al. 2005, He et al. 2019). Several mainstem rivers, however, have undammed tributary rivers that provide access to less-impacted river channel and floodplain habitats (Pracheil et al. 2013, Silva et al. 2019). Moreover, the smaller sizes of tributaries offer several logistical advantages for river conservation, including more manageable scales for restoration, and fewer interjurisdictional boundaries and competing uses (Dolezsai et al. 2015, Laub et al. 2018). Consequently, conservation value of tributaries is increasingly recognized within riverscape-scale management planning (Ziv et al. 2012, Neeson et al. 2015, Winemiller et al. 2016).

The conservation value of tributaries for supporting mainstem fish populations likely depends on the degree to which riverine fishes use tributaries to fulfill critical life-cycle functions (e.g., reproduction, refuge, feeding). However, the mechanisms facilitating tributary use by fishes are often unclear, and most observations are set in smaller, wadeable streams (Osborne and Wiley 1992). The extent of tributary use by mainstem dispersers can depend on species (Schaefer and Kerfoot 2004), life stage (Cathcart et al. 2019), and resistance of local conditions in tributaries to upstream dispersal (Hitt and Angermeier 2008, Ferreira et al. 2019).

Mainstem-tributary movements by fishes can be classified as “limited exchange” (minimal or no exchange), “confluence exchange” (localized movements near confluences), or “network dispersal” (extensive upstream dispersal in tributaries; Thornbrugh and Gido 2010). Thornbrugh and Gido (2010) found little evidence of network

dispersal into wadeable tributaries by mainstem riverine fishes. However, multiple studies suggest larger tributaries might be more conducive to upstream dispersal by mainstem fishes (Grenouillet et al. 2004, Hitt and Angermeier 2008). For example, Hitt and Angermeier (2008) found more extensive dispersal into larger wadeable tributaries from mainstems, especially for “river” species and other mobile fish taxa. Extrapolating findings from Hitt and Angermeier (2008) beyond wadeable streams would suggest rates of tributary use are likely high in nonwadeable rivers and for riverine fishes (Radinger and Wolter 2014).

Differing availabilities of specific habitats within tributaries could cause varying degrees of tributary use among similarly sized tributaries (Cathcart et al. 2019). If habitats within tributaries are redundant with habitats already available in mainstems (i.e., “supplemental” or “substitutable” habitats sensu Dunning et al. 1992, Schlosser 1995), then distributional patterns within tributaries should be structured mainly by the cost of dispersal from mainstems (Miyazono and Taylor 2013, Ferreira et al. 2019). Such dispersal from mainstems should generate nested beta diversity, whereby richness decreases upstream as local assemblages are comprised of sequentially smaller subsets of downstream assemblages (Taylor and Warren 2001). However, riverine fishes could bypass downstream reaches of tributaries if searching for complementary “attractive” (sensu Cathcart et al. 2019) habitats not available in mainstems, resulting in turnover beta diversity (e.g., rocky shoals for spawning; Vokoun et al. 2003, Lyons et al. 2016). Thus, even if local richness (alpha diversity) at sites is similar, beta diversity could vary among tributaries. Moreover, species turnover among reaches could afford higher total richness (gamma diversity) within tributaries and signify availability of both supplemental and complementary habitats within a tributary.

Fine-scale data on fish assemblages and habitats within rivers are often unavailable (Cooke et al. 2012), which creates issues when appraising

the conservation value of nonwadeable tributaries for riverine fishes. The coarse resolution of fish distributional data in part stems from relatively low levels of survey effort within rivers and traditional reliance of many fish assessments on surface- and bank-oriented seining and boat electrofishing, which are unlikely to detect benthic species in deep, turbid rivers (Flotemersch et al. 2011). Macroecological approaches for estimating the capacity of tributaries to support riverine fishes have attempted to overcome insufficient, fine-scale fish and habitat data by downscaling relationships between coarse environmental variables and fish assemblage data aggregated across broad spatiotemporal scales (Xenopoulos and Lodge 2006, Pracheil et al. 2013, Laub et al. 2018). For example, Pracheil et al. (2013) discovered tributaries in the Mississippi River basin with mean annual discharge at mouth $\geq 166 \text{ m}^3/\text{s}$ supported $\geq 80\%$ of potential large-river fish species, thereby providing an easily measured indicator of high-value tributaries. Species–discharge relationships (SDRs), however, are often scale-dependent (McGarvey and Ward 2008), meaning it is unclear whether mean annual discharge consistently predicts large-river fish richness at specific sites *within* tributaries. Ground-truthing whether discharge predicts the extent of upstream tributary use by riverine fishes could help gauge potential outcomes of restored connectivity through barrier removal within tributaries.

Our goal was to contrast tributary-use patterns by large-river specialist (LRS) fishes in two large, but physically dissimilar, tributaries. Large-river specialists are fishes with populations historically centered in the Missouri and Mississippi river mainstems and floodplains. We framed our study with four research questions: (1) Do alpha diversity (mean site-level species richness) and beta diversity (among-site species differences within tributaries) vary between tributaries? (2) Does mean annual discharge correlate with local habitat and downstream distance (i.e., connectivity) to mainstems? (3) Are slopes of SDRs consistent between tributaries? And (4) Do local habitat and downstream distance explain residual richness at sites beyond variation already explained by SDRs? We hypothesized two situations when discharge would underestimate LRS fish richness at sites: (1) low-discharge sites with

high downstream connectivity that are more easily accessed by fish dispersing from Mississippi/Missouri rivers, and (2) low-discharge sites that contain habitats similar to those in Mississippi/Missouri rivers (i.e., presence of large-river habitat). These questions explore unknown mechanisms underpinning mainstem–tributary linkages using rarely available fine-scale fish and habitat data, which will help riverscape conservation planners value the conservation potential of tributaries for LRS fishes.

METHODS

Large-river specialist fishes

Large-river specialists are fishes with distributions historically centered in Mississippi/Missouri River mainstems and floodplains in our study region, so occurrences in tributaries likely stem from migratory individuals fulfilling life-cycle requirements (i.e., spawning, growth, survival) or populations subsidized by dispersal from the Mississippi/Missouri rivers (e.g., source–sink metapopulation dynamics). Our list of LRS species (Appendix S1: Table S1) largely follows Pflieger’s (1989) “big river” fishes guild (candidate LRS spp. = 35 in Grand R., 42 in Meramec R.). At least 15 LRS species are confirmed as migratory (diadromous or potamodromous; O’Hara et al. 2007). Fourteen species have a conservation status of at least “vulnerable” in the study region (NatureServe 2021, Appendix S1: Table S1), with many being impacted by extensive engineering of the Missouri and Mississippi rivers for navigation and flood control (Galat et al. 2005, Schramm et al. 2016).

Some LRS species use tributaries as low-velocity nurseries or refugia (Brown and Coon 1994), while other LRS species have been documented in specific reaches with coarse spawning substrates (Vokoun et al. 2003). Therefore, to gain further insight into potential functional mechanisms underlying distributions of LRS species and diversity patterns, we quantified water-velocity and substrate-size preferences of LRS species based on classifications in Frimpong and Angermeier (2009) and supplemented with natural history descriptions (Pflieger 1997): Rheophilic species (13 spp.) preferred “high” or “moderate currents” (water velocities); lithophilic species (24 spp.) preferred substrate sizes coarser than sand

while avoiding “silt,” “clays,” and “muck.” Alternatively, some LRS fishes may not be mobile enough to move from mainstems into tributaries to exploit tributary habitats; therefore, we used maximum reported total length as a surrogate for mobility (Radinger and Wolter 2014) and categorized species as large-bodied (≥ 250 mm; 24 spp.) or small-bodied (< 250 mm; 18 spp.; Frimpong and Angermeier 2009).

Grand and Meramec river systems

We sampled sites along the lower 200 and 244 km of the Grand and Meramec rivers, which

are nonwadeable tributaries to the Missouri and Mississippi rivers, respectively (Missouri, USA; Fig. 1). Our use of “tributary” refers to the Grand and Meramec river systems (Fig. 2). Both Grand and Meramec rivers also have nonwadeable tributaries (i.e., Shoal Creek, Thompson River, Big River, Bourbeuse River). We refer to Shoal Creek and Thompson, Big, and Bourbeuse rivers as tributary “branches” to distinguish these smaller interior rivers from the larger Grand and Meramec rivers. We refer to the Missouri and Mississippi rivers as “mainstem” large rivers.

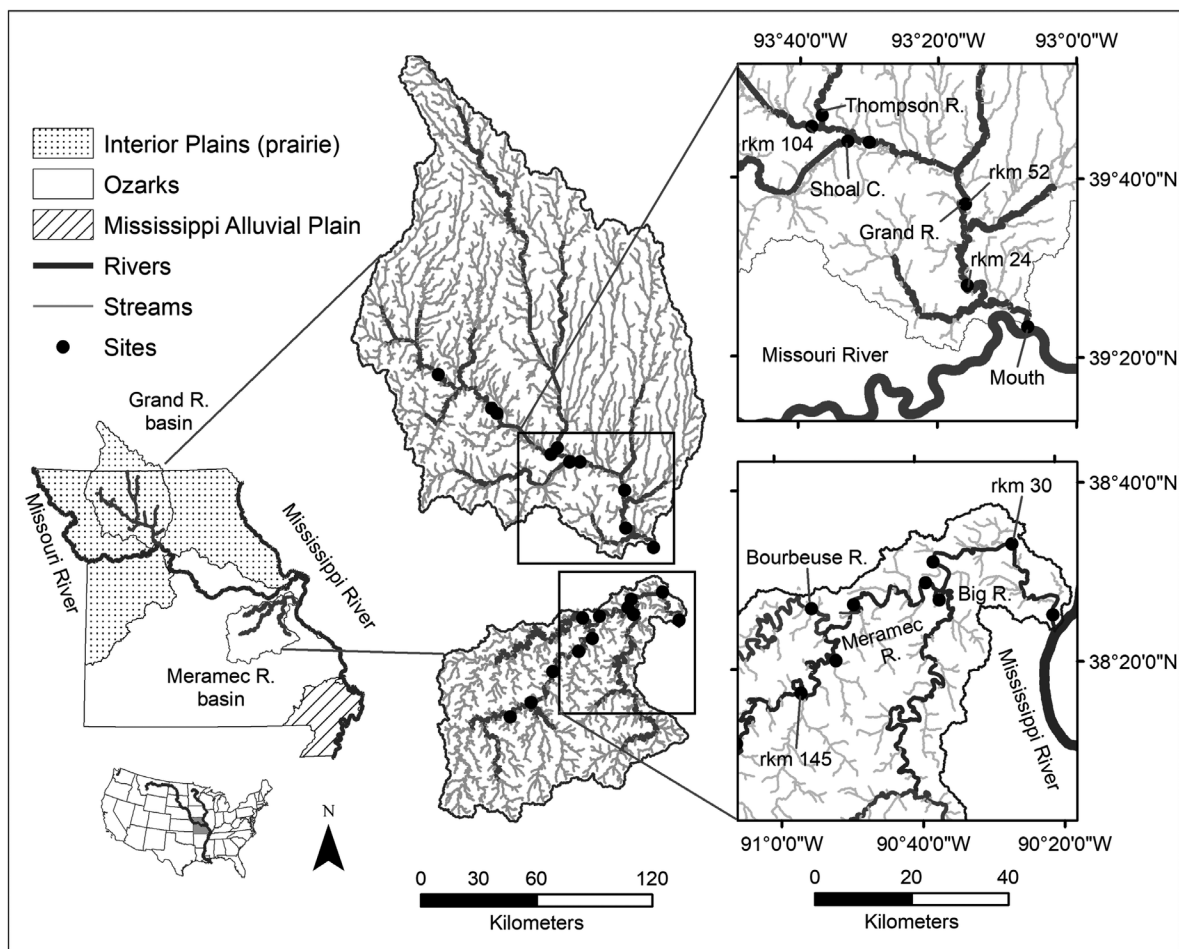


Fig. 1. Sites in the Grand ($N = 10$, prairie region) and Meramec ($N = 12$, Ozark region) river systems surveyed for large-river specialist fish species in 2016 (Missouri, USA). Insets: sites extended at least 1 km away from major confluences. Watercourse distances (river km) are upstream of each river system’s mouth. Shapefile sources: physiographic regions (Missouri Resource Assessment Program), river networks (National Hydrography Dataset version 2), and state boundaries (US Census Bureau).

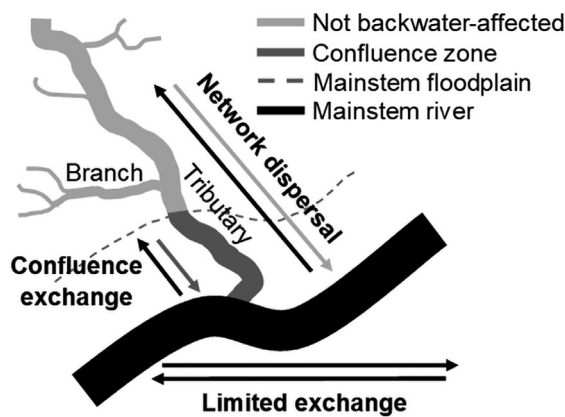


Fig. 2. Conceptual depiction of Thornburgh and Gido's (2010) classification of tributary-use patterns by mainstem fishes: limited exchange = limited or no movements between mainstem and tributary; confluence exchange = localized movements between mainstem and lower tributary reach in the confluence zone within the mainstem's floodplain and with backwater-affected hydrology; and network dispersal = extensive use of tributary upstream beyond the confluence zone. A branch is peripheral river within a tributary system. A tributary system encompasses the main channel of a tributary and constituent branches.

The Grand River is a low-gradient, prairie river draining the Interior Plains region of northern Missouri and contributes 7.9% of discharge to the Missouri River at their confluence (USGS and USEPA 2012; maximum Grand River drainage area = 20,417 km²). The Grand River is turbid and dominated by fine sediments (clay-sand) that form unstable river channels reinforced by woody debris. Most of the Grand River drainage is agricultural (76%, USGS 2014), and much of the main channel is leveed to minimize flooding, but some semi-natural meandering still occurs, especially throughout the lower 60 km.

The Meramec River drains the Ozark Plateau, a topographically diverse, upland region in southern Missouri. Although the Meramec River is nonwadeable (maximum drainage area = 10,270 km²), it contributes only 1.7% of flow to the Mississippi River at their confluence (USGS and USEPA 2012). Sites in the Meramec River have higher habitat diversity and span stronger longitudinal habitat gradients than those the Grand River (Dunn 2020). Channels consist of

well-defined alternating pools and shoals and are semi-confined by bluffs. High groundwater and drainage forest cover (68%, USGS 2014) maintain high water clarity, especially in upstream reaches.

Although the Grand and Meramec rivers broadly differ in habitat, both systems have similar river network configurations. Neither river is impounded in their lower 250 km, such that fish can disperse across broad spatial extents. Further, both rivers span fifth–seventh orders and are joined 62–116 km upstream of their mouths by nonwadeable fifth-order tributary branches in close succession. Network branching teases apart longitudinal distance downstream and discharge by providing low-discharge tributary branches that are near Mississippi/Missouri rivers and thus accessible to dispersing LRS species.

In the Grand River system, we placed eight sites approximately every 25 km along the Grand River (rkm 1–200) and one site in two tributary branches, with lower site boundaries beginning 1 km upstream from the Grand River (Shoal Creek, Thompson River; 10 total sites in Grand River system). We relocated two sites to be within 5 km of the nearest river access due to limited access and navigability. In the Meramec River system, we placed nine sites approximately every 30 km along the Meramec River (rkm 1–244) and added a site (rkm 53) to increase resolution into richness changes near branch confluences. We also had a site in each of the Meramec River's two tributary branches (Big and Bourbeuse rivers; 12 total sites in Meramec River system). All sites in both systems were ≥ 1 km away from major confluences (between \geq fifth-order rivers) to minimize detections of random short-distance dispersers. Although we sampled an additional 44 km farther upstream in the Meramec River, discharge was similar at uppermost sites in both river systems (mean annual discharge at rkm 244 in Meramec River = 19 m³/s; at rkm 200 in Grand River = 22 m³/s).

The Missouri and Mississippi rivers are river mainstems with expansive floodplains that affect habitat within lower reaches of tributaries known as “confluence zones” (Thornburgh and Gido 2010). As such, reaches of the Grand and Meramec rivers within confluence zones are characterized by deep (>2.5 m), wide (>100 m) channels and slow-moving water (<0.1 m/s).

Flows within confluence zones are backwater-affected and partly mediated by surface elevations of the Mississippi/Missouri rivers. Our lowermost sites (1–5 km upstream of mouth) are backwater-affected near constantly, whereas sites farther upstream beyond Mississippi/Missouri River floodplains (Grand R. = rkm 24, Meramec R. = rkm 30) are likely backwater-affected only during high (≥ 80 percentiles) Mississippi/Missouri River surface elevations (Remo et al 2012, USAC 2018).

Fish and habitat sampling

We sampled sites between April and September 2016 with a comprehensive six-gear protocol designed for nonwadeable rivers. Protocols were derived from Dunn and Paukert (2020) and consisted of gear combinations capable of sampling major river habitats (shallow–deep, slow–swift, on–off-channel). Site lengths were approximately 50 mean wetted-channel widths (MWCW) and ranged from 1.5 to 5.0 km. Because river size (i.e., discharge) varied sevenfold across sites, our absolute effort with active-sampling gears was proportional to each site's MWCW, which kept ratios of effort among active gears approximately constant among sites (see Appendix S1: Table S2 for effort by site, Appendix S1: Fig. S1 for georeferenced fish and habitat survey). Active gears were boat electrofishing (11–32 50-m sub-samples equaling 550–1600 total m per site), seining (7–25 10-m hauls per site), and benthic trawling (3–10 50-m sub-samples equaling 150–500 m per site). To distribute effort within sites, each sub-sample was randomly placed within 1 of 10 equal-length sections. We complemented active gears with three passive gears fished overnight and meant to sample difficult-to-sample habitats: (1) one stationary trammel net (30.5 m long \times 1.8 m deep) with 20.3 cm and 9.5 cm bar mesh outer and inner panels, respectively; (2) two non-baited hoop nets (1.2 m diameter) with 3.8 cm bar mesh; and (3) four non-baited mini-fyke nets (3.1 mm bar mesh, two 0.6-m \times 1.2-m frames and 4.5-m lead). Trammel and hoop nets sampled deep pools (>1.5 m), while mini-fyke nets sampled shallower off-channel and/or structurally complex habitats. We first electrofished and set trammel nets in all sites in late spring and early summer to detect adult large-bodied migratory fishes residing in tributaries for

spawning and then seined, trawled, and set hoop and mini-fyke nets throughout summer.

We measured 10 river habitat variables at sites in tributaries and at one site in each of the Missouri and Mississippi rivers (habitat sampled September 26–October 27, 2016). Sites in the Missouri and Mississippi rivers were 5 km long, extending 2.5 km up- and downstream of confluences with Grand and Meramec rivers, respectively. Our habitat protocol was a rapid (<1 d), modified point-transect design based on USEPA (2013). Each site was divided by 21 equally spaced cross-sectional transects spanning the main channel. Along each transect, we placed five equidistant points. We added an additional point at the center of off-channel habitats intersected by transects (≥ 105 total points per site). At each point, we recorded depth, water-column velocity, substrate size, abundance of large woody debris, and whether the point was in a shoal (i.e., steepened channel with swifter, turbulent water than surrounding channel units). Depth was recorded to the nearest decimeter with side-scan sonar (Lowrance HDS-10, Tulsa, OK). We mounted a velocity sensor (Hach FH950, Loveland, CO) to a pole to measure water-column velocity at approximately 60% depth or averaged velocities at 20% and 80% for depths >1 m. In shallow areas, depth and water-column velocity at 60% depth were recorded with a top-setting wading rod. Next, we used size-scan sonar imagery, corroborated by a sounding pole (depths <4 m) or weighted rope (depth ≥ 4 m), to classify predominant substrate into six categories: silt/clay (1 = ≤ 0.06 mm), sand (2 = 0.07–2.0 mm), gravel/pebble (3 = 3.0–64 mm), cobble (4 = 65–256 mm), boulder (5 = ≥ 257 mm), and bedrock (6). We also used side-scan sonar to enumerate large woody debris (≥ 5 m long) and large boulders (≥ 1 m diameter) intersecting a 5 \times 5 m area centered at each point.

Three variables were recorded at the ends of each transect (i.e., two observations per transect): (1) We visually categorized the percentage of shoreline covered by macrophytes within 10 m up- and downstream of each transect (0 = $\leq 5\%$, 1 = 6–25%, 2 = 26–50%, 3 = 51–75%, 4 = $>75\%$); (2) we categorized whether the riparian area extending 25 m from the river bank was confined by rock bluffs (i.e., restricted floodplain hereafter

called “confinement”); and (3) we visually estimated the percentage of shoreline (lengthwise) between consecutive transects with off-channel areas with surface-water connections to the main channel, which was corroborated by satellite imagery. We also measured turbidity once per site as Secchi depth in a well-lit area using polarized glasses. Finally, we summarized point- and transect-based variables at a site level by calculating means or percentages of habitat observations.

ANALYSES

Spatial variation in tributary use

We used two approaches to describe and contrast tributary-use patterns between rivers. First, we used Thornbrugh and Gido’s (2010) three-category scheme to classify the upstream extent of tributary use by LRS species (see conceptual depiction Fig. 2). We considered species not caught by our sampling as evidence for *limited exchange* between tributaries and Mississippi/Missouri rivers (italicized terms are in Fig. 2). Species caught in backwater-affected confluence zones (lowermost sites = rkm 1–5) conformed to *confluence exchange*, and species dispersing upstream in tributaries beyond confluence zones supported *network dispersal* (\geq rkm 24 in Grand R., \geq rkm 30 in Meramec R.). This scheme also corresponds with major hydrogeomorphic habitat changes, whereby sites upstream of confluence zones have higher habitat diversity (i.e., varying depths, substrates, water velocities), while sites within confluence zones are more uniformly deep, slow, and dominated by fine sediments (Dunn 2020). Because we suspected LRS species were using tributaries and specific reaches for different purposes, we calculated percentages of species that were rheophilic, lithophilic, or large-bodied at our lowermost sites (confluence exchange), sites upstream of our lowermost sites (network dispersal), and species not detected in tributaries (limited exchange). For example, the species list for confluence exchange was composed of all species sampled at the lowermost site (rkm 1–5) within each tributary, while the species list for network dispersal was developed by pooling LRS species sampled at sites upstream of each tributary’s confluence zone site (Meramec R. = rkm 30–244; Grand R. = rkm 24–199).

Second, we calculated total LRS richness detected in each tributary system (gamma diversity), average site-level LRS richness (alpha diversity), and among-site species compositional differences (beta diversity). We used the “betapart” R package (Program R version 4.0) (Baselga and Orme 2012) to deconstruct beta diversity (Sørensen’s presence–absence index) into two constituents: (1) nestedness (β_{nes}), which is beta diversity created solely by uneven richness across sites. In river systems, nestedness is often associated with increasing dispersal limitation as connectivity and/or habitat suitability decreases when moving away from species-rich sources (e.g., mainstem) to species-poor areas farther upstream in tributary systems (Taylor and Warren 2001, Roberts and Hitt 2010, Ferreira et al. 2019); and (2) spatial turnover (β_{tur}), which is beta diversity created by species replacements (Simpson’s index) and often associated with assemblage responses to varying availabilities of habitats among sites (Miranda et al. 2018).

Species–discharge relationships and residual analysis of large-river specialist richness

Before examining relationships between LRS richness and discharge, we calculated expected mean annual discharge at study sites. We used long-term (1920–2016) discharge data from six (Grand R.) and five (Meramec R.) flow gages to estimate relationships between discharge and drainage area within each basin. Mean annual discharge at sites closely aligned with drainage area in both systems after accounting for drainage-specific slope terms in a linear regression ($R^2 > 0.99$; Appendix S1: Fig. S2). Therefore, we subsequently predicted mean annual discharge at each site from drainage areas reported by the National Hydrography Dataset plus version 2 (USGS and USEPA 2012). Mean annual discharge at lowermost gages in 2016 during sampling was not abnormally high or low (Grand River = 59th percentile, Meramec River = 69th percentile).

We used a two-step process that estimated SDRs within tributaries and then tested whether unexplained residual variation in LRS richness at sites was further explained by habitat and downstream distance to Mississippi/Missouri rivers (i.e., metric for mainstem connectivity). In the first step, we constructed SDRs to examine

whether discharge explained richness within tributaries and whether model slopes of SDRs varied between tributaries. The former model (i.e., identical SDR slopes between rivers) represents a *status quo* SDR approach that solely uses discharge to predict fish species richness in tributaries without accounting for among-tributary differences (e.g., Xenopoulos and Lodge 2006, Pracheil et al. 2013). Our candidate model set included linear regressions between LRS richness (response variable) and river (factor coded as 0 for Grand R. and 1 for Meramec R.), discharge, discharge², and interactions between discharge-metrics and river (i.e., seven candidate models plus intercept-only model). We included quadratic discharge terms because flow–ecology relationships are often nonlinear (Rosenfeld 2017). We treated each model as a competing hypothesis and evaluated relative model support among hypotheses using Akaike’s information criterion corrected for small sample size (AICc). Although LRS richness is a count data type (response variable), linear regressions were more supported than Poisson generalized linear models.

We generally expected positive SDRs in step 1, but we hypothesized discharge would underestimate richness in low-discharge sites with high mainstem connectivity and sites containing large-river habitats resembling habitats in the Mississippi/Missouri rivers. Therefore, in step two, we linearly regressed the ordinary residuals extracted from the best-supported model in step

1 to metrics for downstream connectivity and large-river habitat. We quantified downstream connectivity as watercourse distance to the Missouri (Grand R.) or Mississippi (Meramec R.) rivers. We calculated large-river habitat similarity by first performing a principal component analysis (PCA) on a correlation matrix of habitat data (10 variables) from both rivers combined. Then, we calculated the inverse of Euclidean distances between multivariate centroids of sites to those of either Missouri (reference for Grand R.) or Mississippi (reference for Meramec R.) river based on principal component (PC) axes with eigenvalues >1. Thus, sites with habitats resembling those in the Mississippi or Missouri river had shorter multivariate distances, but after taking their inverses, these sites had larger values for large-river habitat. We also included each constituent PC axis (eigenvalues >1) as candidate predictor variables. Before performing PCA, we reduced skew of five habitat variables via normalizing transformations (Table 1). Finally, we linearly regressed residual LRS richness against each predictor variable and evaluated relative support among predictors against an intercept-only (*null*) model with AICc.

RESULTS

Tributary-use patterns and diversity partitioning

We collected most of the potential pool of LRS species in the Grand (18 of 35 LRS spp., 51%;

Table 1. Habitat variables recorded at 24 sites in the Grand ($N = 10$), Meramec ($N = 12$), Missouri ($N = 1$), and Mississippi ($N = 1$) rivers in 2016 (Missouri, USA).

Variable	Unit	Scale	Transformation	Pearson correlations (r)		
				PC1 (49%)	PC2 (20%)	PC3 (11%)
Boulder	Count	Point	$\text{Log}(x + 0.1)$	−0.76	0.56	−0.20
Confinement	%	Transect	$\text{Arcsine } \sqrt{x}$	−0.92	0.07	−0.05
Large wood	Count	Point	–	−0.41	−0.31	−0.71
Macrophytes	Ordinal	Point	–	−0.93	−0.11	−0.02
Off-channel	%	Transect	$\text{Arcsine } \sqrt{x}$	−0.62	0.63	0.17
Secchi depth	m	Site	–	−0.77	−0.36	0.14
Shoal habitat	%	Point	–	−0.78	−0.40	−0.03
Substrate size	Ordinal	Point	–	−0.86	−0.01	0.08
Water depth	m	Point	$\text{Log}(x + 0.1)$	0.19	0.87	−0.42
Water velocity	m/s	Point	\sqrt{x}	−0.31	0.34	0.55

Notes: “Scale” refers to the grain size at which variables were recorded. All variables were summarized to sites, and five variables were transformed to reduce skew before performing a principal component (PC) analysis. Pearson product-moment correlations (r) are between transformed or untransformed (–) variables and PC axes. Boldface indicates the PC axis most correlated with each habitat variable. Percentages of multivariate variation explained by each PC axis are in parentheses.

sites = 10) and Meramec (29 of 42 LRS spp., 69%; sites = 12) river systems. Thus, the 17 and 13 species that were not detected by us in the Grand and Meramec river systems were categorized as *limited exchange*, respectively. Most LRS species observed within tributaries ranged upstream beyond confluence zones (Grand R. = 17 of 18 spp., 94%; Meramec R. = 23 of 29 spp., 79%), supporting *network dispersal* as the predominant distributional pattern. Only one (6%) and six (20%) species were solely detected in confluence zones (i.e., conforming to *confluence exchange*) in the Grand and Meramec rivers, respectively (Table 2).

Percentages of LRS rheophilic fishes observed in tributaries were lower (confluence exchange, Grand R. = 20%, Meramec R. = 21%; network dispersal, Grand R. = 24%, Meramec R. = 26%) than species not observed in tributaries (limited exchange, Missouri R. = 41%, Mississippi R. = 39%), indicating water velocities within tributaries may not be sufficient to attract some species into tributaries (Fig. 3). Similarly, percentages of lithophilic species were lower in the fine sediment-dominated Grand River (confluence exchange = 47%, network dispersal = 47%) than LRS species not collected in the Grand River (limited-exchange species = 65% lithophilic). In contrast, percentages of lithophilic LRS species were higher in the Meramec River system (confluence exchange = 58%, network dispersal =

74%) than LRS species exhibiting limited exchange in the Mississippi River (limited exchange = 39%), indicating coarse substrates in the Meramec River may be sources of attractive complementary habitat for fishes, especially in sites upstream of confluence zones. Finally, richness of LRS fishes was increasingly composed of large-bodied species (total length ≥ 250) for dispersal categories farther upstream in both Grand (limited exchange = 53%, confluence exchange = 67%, network dispersal = 71%) and Meramec rivers (limited exchange = 38%, confluence exchange = 63%, network dispersal = 70%; Fig. 3).

Although local species richness was higher in the Grand River (12.5 spp. in Grand R. vs. 9.8 spp. in Meramec R.), beta diversity was nearly three times higher in the Meramec River system (0.18 in Grand R. vs. 0.56 in Meramec R.; Table 3). Beta diversity coefficients between LRS fishes in confluence zones (rkm 1–5) and those at sites upstream revealed generally higher spatial turnover in downstream reaches indicative of assemblage responses to varying habitats among sites and higher nestedness in upstream reaches indicative of dispersal limitation (Fig. 4). For example, beta diversity between lowermost sites and those upstream of rkm 145 was entirely comprised of nestedness in both systems. However, the magnitudes of beta diversity coefficients was much lower in the Grand River system. Thus, although longitudinal patterning of beta diversity within both systems was similar, both LRS richness and species composition were more similar among sites throughout the Grand River system compared to the Meramec River system.

Table 2. Large-river specialist (LRS) fish tributary-use patterns in the Grand and Meramec river systems in 2016 (Missouri, USA).

Category	Grand river	Meramec river
Candidate large-river specialist species	35	42
Limited-exchange species	17	13
Confluence-exchange species	1	6
Network-dispersal species	17	23

Notes: Candidate LRS species are species with distributions historically centered in the Missouri and/or Mississippi rivers (listed in Appendix S1: Table S1). Species with limited-exchange distributional patterns were not detected by our surveys. Confluence exchange distributional patterns were for LRS species only detected at our lowermost sites in backwater-affected confluence zones (river km 1–5 from mouth). Species that exhibited network dispersal were found upstream of confluence zones (\geq river km 24 in Grand R., \geq river km 30 in Meramec R.).

Relationships between discharge, and habitat and downstream distance to mainstems

Three PC axes had eigenvalues >1 and collectively explained 80% of variation in among-site habitat within and among tributaries (Fig. 5): PC1 (49%) integrated several longitudinal gradients associated with the downstream transition from upstream to downstream habitats based on maximum absolute values of Pearson product-moment correlations (r) with coarse substrate, channel confinement, low turbidity, and numbers of boulders, shoals, and macrophytes (Table 1); PC2 (20%) reflected increasing off-channel areas and depth; PC3 (11%) represented increasing

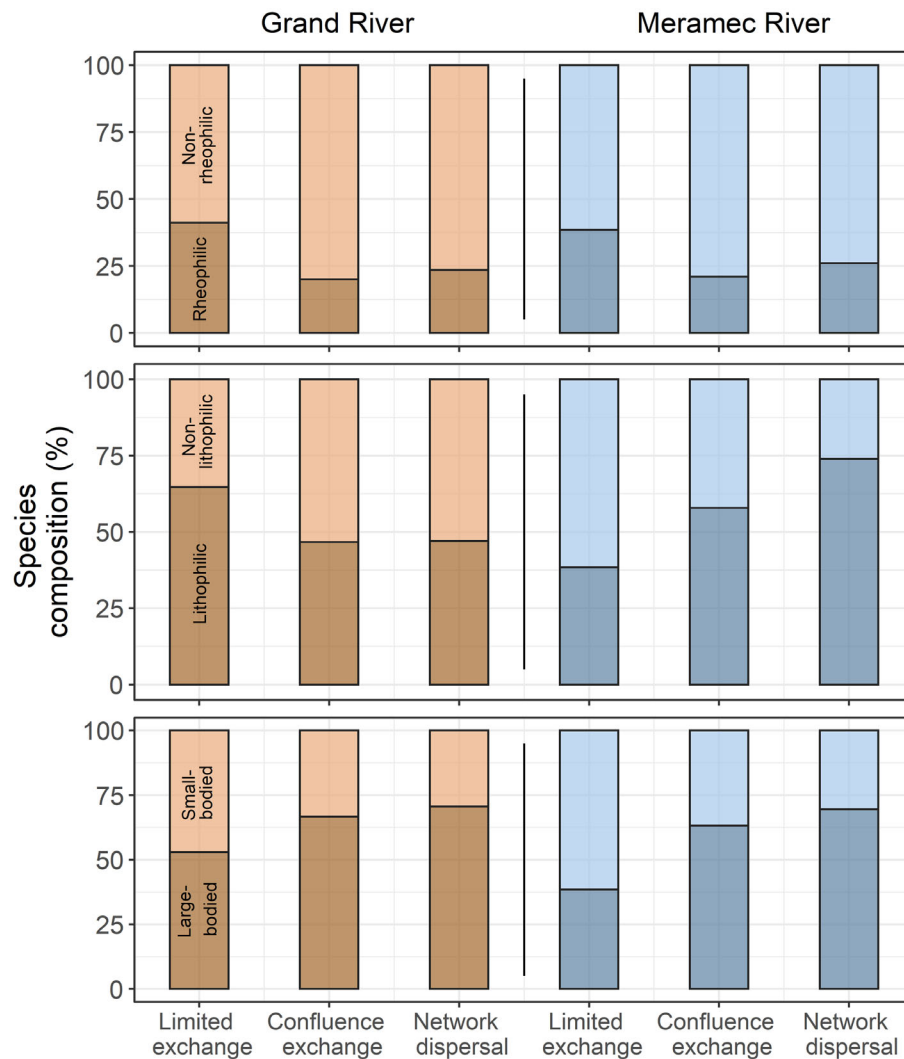


Fig. 3. Percentages of large-river specialist fishes with preferences for swift water velocities (rheophilic) and coarse substrates (lithophilic) and by total length (body size) within different reaches of the Grand River system (35 candidate species, 10 sites) and Meramec River system, USA (42 candidate species, 12 sites). The Grand and Meramec rivers are tributaries to the Missouri and Mississippi rivers, respectively. Species conforming to limited exchange occur in the Missouri and/or Mississippi rivers but were not detected in tributaries by fish sampling in 2016. Percentages for confluence exchange are for species detected at lowermost sites within backwater-affected confluence zones (river km 1–5) of tributaries. Percentages for network dispersal are for species from sites upstream beyond confluence zones in tributaries.

water velocities and decreasing large woody debris. Overall, habitats in the Grand and Missouri rivers were more similar than habitats in the Meramec and Mississippi rivers (Fig. 5, see Appendix S1: Table S3 for habitat data). An exception was the lowermost site in the Meramec

River confluence zone, which grouped with Grand River sites closer to reference large-river habitat in the Mississippi/Missouri rivers. Absolute value of Pearson product-moment correlations (r) between discharge, and large-river habitat and downstream distance of sites to each

Table 3. Diversity partitioning of large-river specialist fishes detected in the Grand and Meramec river systems in 2016 (Missouri, USA).

Diversity component	Grand river	Meramec river
Large-river specialists (γ diversity)	18	29
$\bar{\alpha}$ diversity	12.5	9.8
β diversity	0.18	0.56
β_{tur} diversity	0.05	0.12
β_{nes} diversity	0.13	0.44

Notes: Gamma (γ) diversity is the total species richness detected by our surveys within each tributary. Alpha diversity ($\bar{\alpha}$) is mean local richness at sites within each tributary. Beta diversity (β) is among-site species compositional heterogeneity and was partitioned into heterogeneity generated by among-site replacements of species (turnover, β_{tur}) and uneven species richness across sites (nestedness, β_{nes}).

system's river mouth were ≥ 0.76 in both systems, indicating discharge is a coarse metric for both habitat availability and downstream connectivity

to a mainstem river (Fig. 6). Meramec River sites along PC1 (upstream–downstream gradient) were positively correlated with mean annual discharge ($r = 0.42$), whereas the Grand River's correlation coefficient was slightly negative ($r = -0.06$) likely because of a lack of upland habitats in the Grand River system (Fig. 1). Signs and magnitudes of correlations between PCs 2 ($r \geq 0.80$) and 3 ($r \leq 0.36$) and mean annual discharge were generally consistent between rivers (Fig. 6).

Species–discharge relationships and residual analysis

Models that assumed identically sloped SDRs in the Grand and Meramec river systems (i.e., *status quo*) indicated LRS richness increased with discharge ($R^2 = 0.46$; Fig. 7 top panel); however, a model that allowed linear SDRs to vary between tributary systems was better supported (Akaike weight of top-ranked model [w_1] = 0.82)

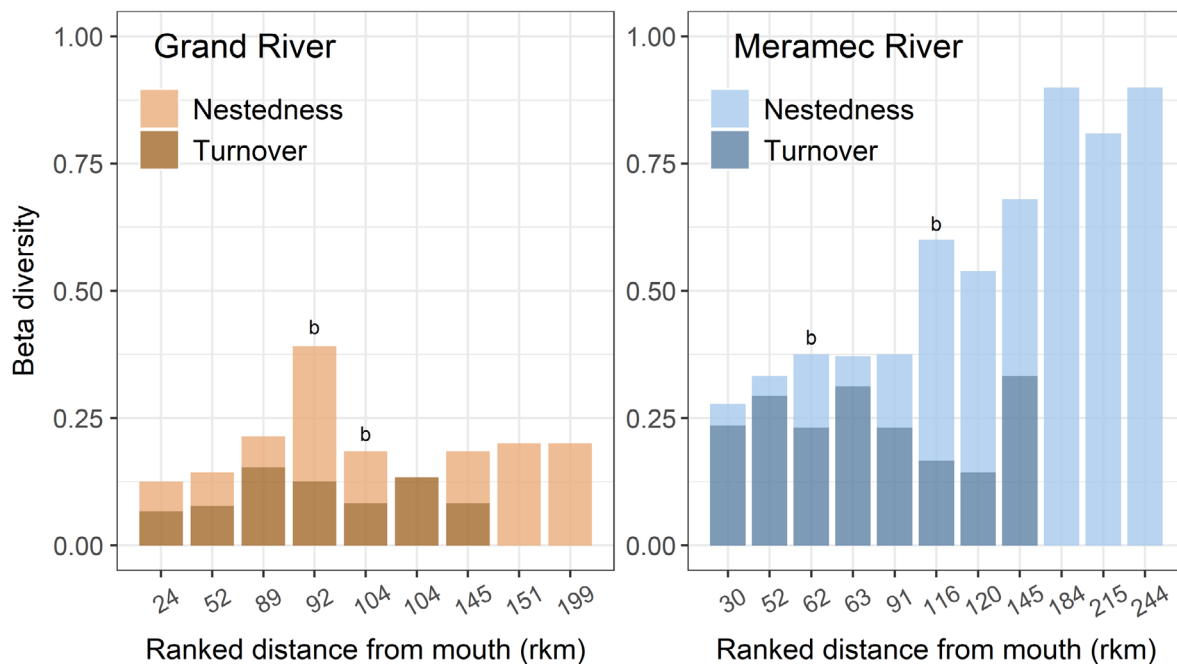


Fig. 4. Beta diversity coefficients between fish assemblages at lowermost sites (river km 1–5) in confluence zones of the Grand and Meramec rivers vs. fish assemblages at sites upstream beyond confluence zones in 2016 (Missouri, USA). Nestedness (component of Sørensen's index) is beta diversity generated by uneven richness between sites and is indicative of dispersal limitation upstream. Turnover (Simpson's index) is beta diversity generated by constant richness with species replacements among sites and is indicative of assemblage responses to varying habitats among sites.

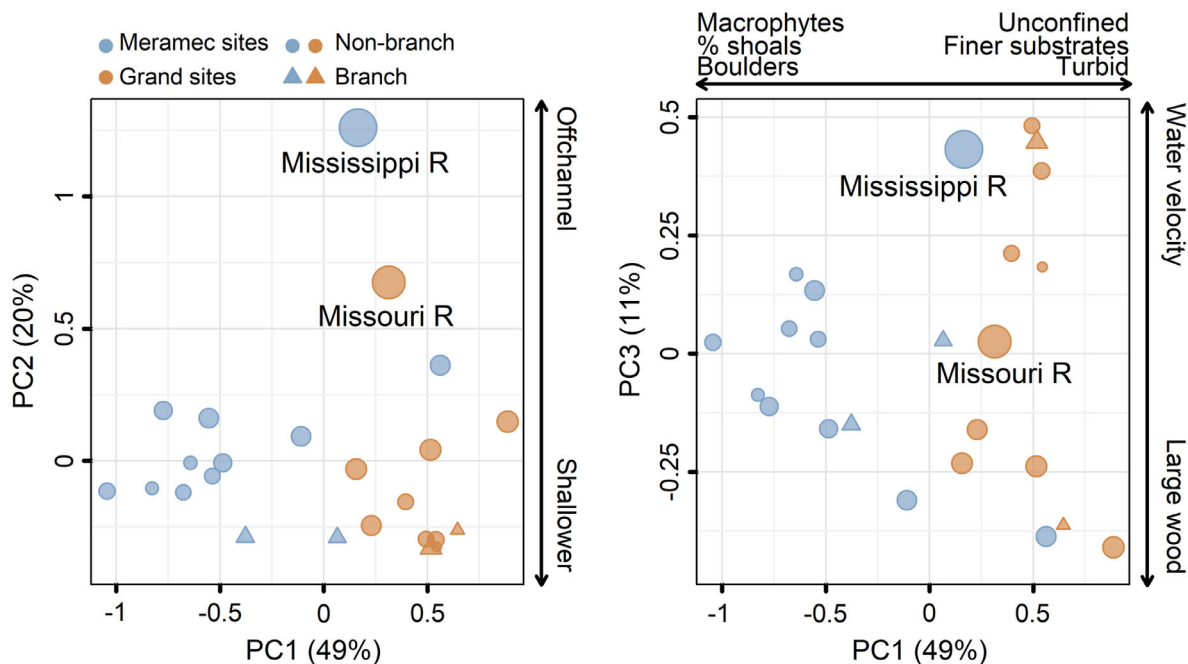


Fig. 5. Principal components (PC) of 10 habitat variables (Table 1) from 24 sites in the Grand ($N = 10$), and Meramec ($N = 12$) river systems, and Missouri ($N = 1$) and Mississippi ($N = 1$) rivers (USA). Points are proportional to the natural log of mean annual discharge (m^3/s). Mississippi/Missouri River habitat similarity was the inverse of Euclidean distance of sites to reference large-river habitat in the Missouri (Grand R.) or Mississippi (Meramec R.) rivers in multivariate space.

and explained more variation (river \times discharge interaction $[\beta \pm \text{SE}] = 0.14 \pm 0.04$, $R^2 = 0.71$; Table 4; Fig. 7 middle panel). In the Grand River system, species richness changed more gradually with discharge than in the Meramec River system. For example, LRS richness at the mouths of both rivers was comparable (Grand R. = 15 spp., Meramec R. = 19 spp.). However, we detected only 1–2 species at three lower-discharge sites (19–37 m^3/s) upstream of rkm 145 in the Meramec River system, while we detected 10 LRS species at both lower-discharge sites (22–39 m^3/s) upstream of rkm 145 in the Grand River system. Predictor variables and parameter estimates for models are in Appendix S1: Tables S4 and S5, respectively.

Analyzing residuals of SDRs from the best-supported model in the first modeling step revealed discharge alone underestimated LRS richness in low-discharge sites in tributary branches with high downstream connectivity, while overestimating richness in more isolated

upstream sites (Table 5; Fig. 7 bottom panel). The model with a linear effect of downstream distance to river mouth ($\beta_{\text{distance}} = -0.02 \pm 0.01$, $\Delta\text{AICc} = 0.0$, $w_1 = 0.51$, $R^2 = 0.20$) was better supported than the intercept-only model ($\Delta\text{AICc} = 2.2$, $w_3 = 0.17$, $R^2 = 0.00$). Underestimated richness was most apparent near Meramec River–tributary-branch confluences in the Meramec River system; low-discharge tributary branches at rkm 62 (Big R.) and rkm 116 (Bourbeuse R.) that were close to the Mississippi River supported 8.7 and 3.2 more LRS species than predicted by discharge, respectively. Further, main-channel Meramec River sites located at rkm 63 and rkm 92 (immediately upstream of the Meramec River–Big River confluence) had 3.2 and 0.7 more species than expected, indicating spatial effects taper with distance upstream of confluences. Neither large-river habitat nor habitat PC axes were better supported than the intercept-only model, indicating discharge entirely represented underlying effects of habitat on LRS

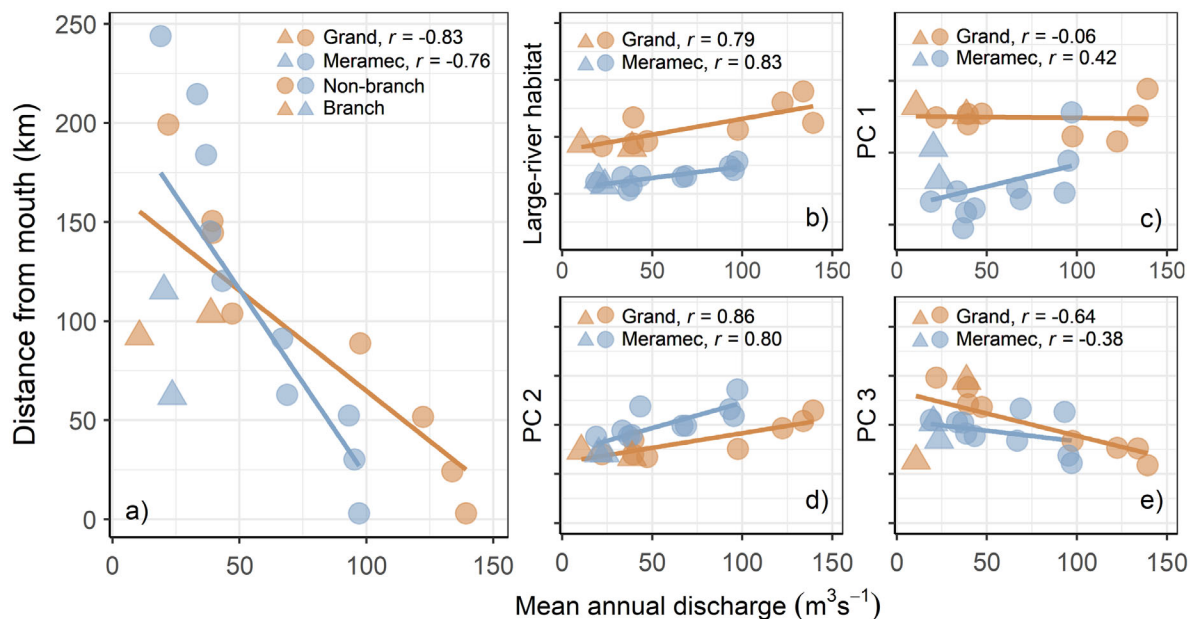


Fig. 6. Pearson product-moment correlations (r) between mean annual discharge at sites and variables potentially explaining large-river specialist fish richness in the Grand ($N = 10$ sites) and Meramec ($N = 12$ sites) river systems sampled in 2016 (Missouri, USA). (a) Distance from mouth is watercourse distance of sites in tributaries to the Missouri (Grand R.) or Mississippi (Meramec R.) rivers. (b) Large-river habitat is the inverse Euclidean distance of habitat at tributary sites to reference large-river habitat in the Missouri (Grand R.) or Mississippi (Meramec R.) rivers in principal component (PC) space constructed from 10 instream habitat variables and three PC axes. (c–e) relationships between discharge and individual PC axes. Correlations between PC axes and individual habitat variables are in Table 3. Branches are smaller, peripheral tributaries to the Grand or Meramec rivers.

richness in both rivers ($\Delta\text{AICc} \geq 3.9$, $w_{3-6} \leq 0.05$ – 0.08 , $R^2 = 0.00$ – 0.04 ; see Appendix S1: Table S6 for parameter estimates).

DISCUSSION

We documented limited-exchange, confluence-exchange, and network-dispersal tributary-use patterns by LRS fishes in two physiographically contrasting nonwadeable tributaries of large rivers. We suspect at least two riverscape attributes contributed to observed spatial variation in tributary use: the availability of (1) supplemental habitats within tributaries similar to those in the Mississippi/Missouri rivers and (2), complementary, but critical, habitats within tributaries that are either naturally lacking or anthropogenically reduced within Mississippi/Missouri rivers. Discharge and the physiographic context of tributaries govern the availabilities of supplemental and complementary habitats within tributaries.

In turn, availabilities of these habitats likely affected the distributional patterns of LRS species within tributaries and whether species used tributaries altogether.

Upstream extent of tributary use by large-river specialist fishes

We detected most LRS species within the Grand (94% of spp.) and Meramec (80% of spp.) river systems upstream beyond backwater-affected confluence zones, demonstrating network dispersal was the predominant tributary-use pattern. This finding in nonwadeable tributaries extends findings from Hitt and Angermeier (2008), who found more extensive upstream dispersal by fish within larger wadeable tributaries. The combination of deep habitats (Roberts and Hitt 2010) and availability of lower velocity resting areas and swimways are important for fish dispersal upstream (McElroy et al. 2012). Consequentially, riverine habitats

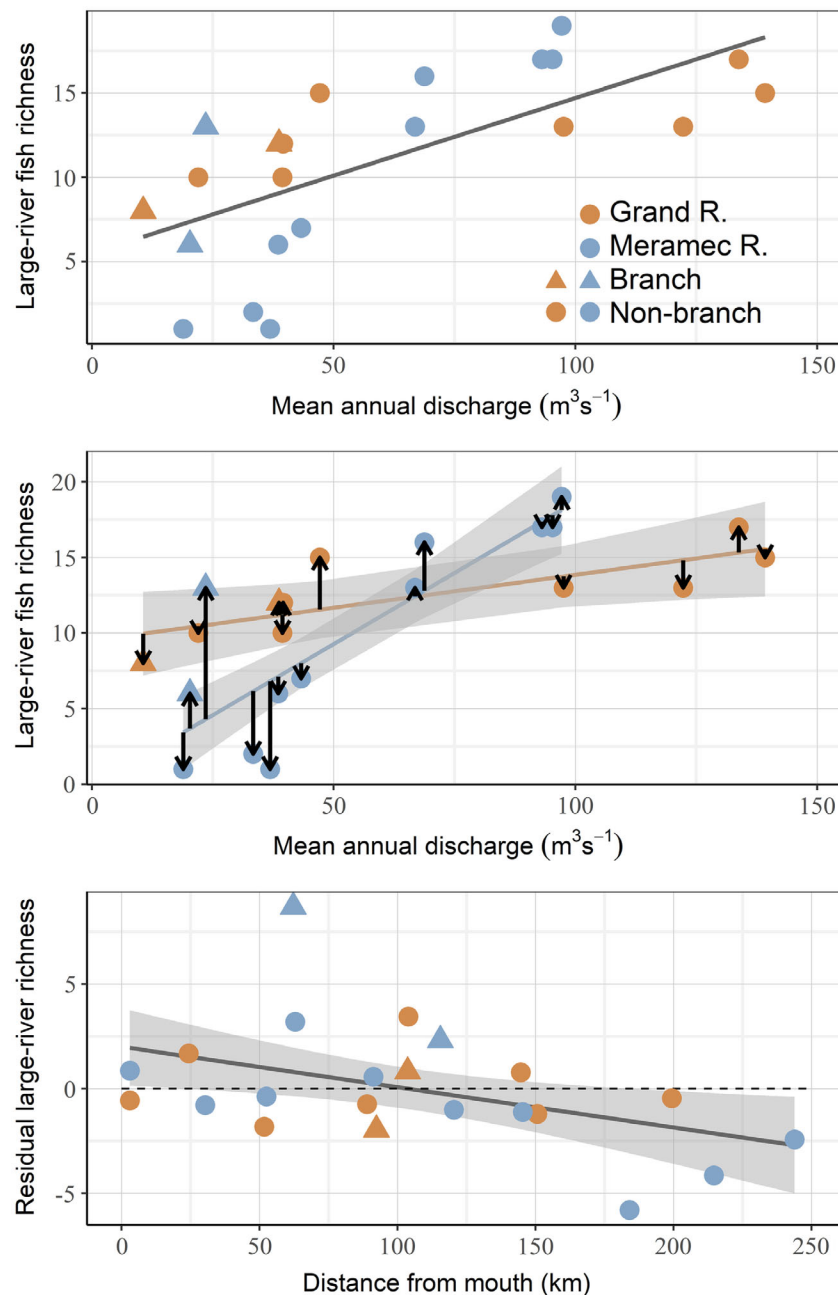


Fig. 7. (Top panel) Species–discharge relationships (SDR) between mean annual discharge and large-river specialist fish richness at 22 sites in the Grand ($N = 10$) and Meramec ($N = 12$) rivers in 2016 (Missouri, USA). (Top) Assuming tributary systems have identical SDRs (*status quo* SDR approach) results in grouped residuals, indicative of a missing grouping effect for different tributaries. (Middle panel) SDRs with tributary-specific slopes and 90% confidence intervals. Black arrows depict residual errors and heteroscedasticity from failing to account for downstream connectivity to mainstem dispersal sources. (Bottom panel) Relationship between residuals of SDRs from middle panel and distance from the mouth of the Grand River (Missouri R. confluence) and Meramec River (Mississippi R. confluence). Residuals above and below 0 indicate where LRS richness was underestimated and overestimated by SDRs in middle panel, respectively.

Table 4. Description and evaluation for alternative models (*i*) for relationships between mean annual discharge (m^3/s) and large-river specialist fish richness (response) detected at sites in the Grand ($N = 10$) and Meramec ($N = 12$) river systems in 2016 (Missouri, USA).

Model	<i>K</i>	Log-likelihood	ΔAICc	w_i	w_1/w_i	R^2
Discharge \times River	4	-54.2	0.0	0.82	1.0	0.71
Discharge ² \times River	5	-54.2	3.8	0.12	6.8	0.71
Discharge	2	-60.9	7.0	0.03	27.3	0.46
Discharge ²	3	-59.7	7.6	0.02	41.0	0.52
Discharge ² + River	4	-58.5	8.7	0.01	82.0	0.57
Discharge + River	3	-60.6	9.4	0.01	82.0	0.47
Intercept-only (null)	1	-67.7	17.8	<0.01	>1000	0.00
River	2	-66.9	19.1	<0.01	>1000	0.07

Notes: Lower delta Akaike information criterion (ΔAICc) and higher model weights (w_i) indicate more support for models. "River" is a grouping factor indicating separate relationships were fit for the Grand (reference level) and Meramec river systems. *K* is the number of model parameters. Evidence ratio (w_1/w_i) is number of times the top model is better supported over lower-ranked models. Parameter estimates ($\beta \pm$ standard error) for top-ranked model: intercept = 9.50 ± 1.78 , Discharge = 0.04 ± 0.02 , River = -9.62 ± 2.61 , Discharge \times River = 0.14 ± 0.04 . Parameter estimates of all models are in Appendix S1: Table S5.

Table 5. Descriptions and evaluation for models (*i*) explaining residual large-river specialist fish richness from the best-supported model (Discharge \times River) in Table 4 from data collected from the Grand ($N = 10$ sites) and Meramec ($N = 12$ sites) rivers in 2016 (Missouri, USA).

Model	<i>K</i>	Log-likelihood	ΔAICc	w_i	w_1/w_i	R^2
Distance to river mouth	2	-51.8	0.0	0.56	1.0	0.20
Intercept-only (null)	1	-54.2	2.2	0.19	3.0	0.00
Principal component 1	2	-53.7	3.9	0.08	7.0	0.04
Principal component 2	2	-53.8	4.1	0.07	8.0	0.03
Principal component 3	2	-54.2	4.9	0.05	11.2	0.00
Large-river habitat	2	-54.2	4.9	0.05	11.2	0.00

Notes: Distance to river mouth (downstream connectivity) is the downstream watercourse distance (km) of tributary sites to mouths of the Grand or Meramec rivers. Large-river habitat is the inverse of Euclidean distance in multivariate space defined by three principal component axes between habitat at sites and reference large-river habitat in the Missouri (Grand R.) or Mississippi (Meramec R.) river. Lower delta Akaike information criterion (ΔAICc) and higher model weights (w_i) indicate more support for models. *K* is the number of model parameters. Evidence ratio (w_1/w_i) is the number of times the top model is better supported over lower-ranked models. Parameter estimates ($\beta \pm$ standard error) for top-ranked model: intercept = 2.01 ± 1.07 , Distance to river mouth = -0.02 ± 0.01 . Parameter estimates for all models are in Appendix S1: Table S6.

such as low-velocity pools, meanders, deeper shoals, and lateral areas may explain physical mechanisms facilitating more extensive tributary use in our rivers than previously documented in Wadeable rivers and streams.

In addition to the physical mechanisms of rivers that facilitate tributary use, rates of tributary use among LRS species could be inherently high because many LRS species have dispersal-dependent life histories reliant on exploiting habitat patches spread throughout riverine networks (i.e., "periodic" strategists; Winemiller 2005). For example, prevalent traits among LRS species indicative of wide-ranging life cycles include large body sizes beneficial to movement

(Radinger and Wolter 2014), long generation times (Winemiller 2005), and drift-dependent early life stages (Perkin and Gido 2011). Hence, tributaries could be important habitat sources within the scopes of several LRS species' expansive life cycles (McIntyre et al. 2015).

We detected most LRS species in tributaries, but our surveys indicated tributary use by at least some LRS species is limited within our study area (i.e., some support for the limited-exchange tributary-use pattern). Limited-exchange species were disproportionately small-bodied compared to species exhibiting network dispersal or confluence exchange tributary-use patterns. Small body size (i.e., total length) could

reflect insufficient dispersal abilities to move seasonally into tributaries and/or life histories less dependent on long-distance migration (i.e., non-“periodic” strategists, Winemiller 2005). By exclusively specializing in mainstems, these species could be disproportionately susceptible to physical and hydrologic alterations in the lower Missouri and middle Mississippi rivers. For example, Sturgeon Chub *Macrhybopsis gelida* and Flathead Chub *Platygobio gracilis* are small-bodied LRS species exhibiting limited-exchange patterns that are listed as “vulnerable” and “critically imperiled” in our study region, respectively (Appendix S1: Table S1). In contrast, Flathead Chub is more abundant in the upper Missouri River region where the species seasonally uses tributaries for spawning and as nurseries (Walters et al. 2014).

For some LRS species known to use tributaries, it is possible that tributaries are not equivalent substitutes for the large-river habitat within Mississippi/Missouri rivers. For example, only 11% of Blue Catfish *Ictalurus furcatus* and <13% of Paddlefish *Polyodon spathula* in the middle Mississippi River have natal origins in tributaries (Laughlin et al. 2016, Rude and Whitley 2019). Ultimately, because life cycles of many LRS species transcend both tributaries and mainstems (e.g., Pracheil et al. 2019), the value of tributaries for many LRS species likely depends on the condition of Mississippi/Missouri rivers and vice versa.

Among-tributary differences in habitat and beta diversity

Correlations between discharge and instream habitat PCA axes indicated discharge is likely a coarse surrogate for habitat at sites within tributaries. Riverine habitats, however, are also created by other regional-scale (e.g., geologic, topographic, climatic) and finer-scale (e.g., channel confinement, terrestrial linkages) factors (Ward et al. 2002). Therefore, longitudinal habitats could vary among similarly sized tributaries with different geologic histories and drainage contexts and lead to among-tributary differences in fish diversity patterns.

Beta diversity, indicative of among-site differences in LRS fish assemblages, was higher in the Meramec River system than in the Grand River system. Stark contrasts between habitats within

the Meramec River’s backwater-affected confluence zone and upstream sites in non-backwater-affected reaches likely contributed to the Meramec River system’s higher beta diversity via higher turnover. Tributary confluence zones function as corridors (Neely et al. 2010), supplemental foraging habitats (e.g., Braaten and Guy 1999), and complementary low-velocity nurseries and backwaters for mainstem LRS fishes (e.g., Brown and Coon 1994, Naus and Reid Adams 2018). Confluence zones of both rivers had slow water velocities and many fine-grained substrates (clay–sand). A slightly higher percentage of rheophilic fishes and a markedly higher percentage of lithophilic fishes at sites upstream of the Meramec River confluence zone indicated these non-backwater-affected reaches could provide complementary spawning habitats (i.e., swift, rocky shoals) for migratory LRS species dependent on flow and coarse substrates (e.g., Lyons et al. 2016). Non-backwater-affected reaches are likely particularly important for shoal-dependent LRS species given these habitats have been greatly reduced in large rivers (Galat and Zweimuller 2001). Consequently, these vestiges of rocky large-river habitat may now function as remaining distributional refugia capable of supporting small populations of some LRS species (e.g., River Darter *Percina shumardi*, Western Sand Darter *Ammocrypta clara*).

Some complementary rocky and swift-water habitats also exist upstream of the confluence zone in the Grand River system (e.g., Vokoun et al. 2003) but to a lesser degree, evidenced by the overall similarity of habitats in the Grand River system to those in Missouri River and similar lithophilic trait frequencies of LRS fishes between reaches in the confluence zone and those upstream. Alternative forms of landscape complementation in the Grand River system could be free-flowing, unchannelized reaches with prairie habitats that allow early life stages to drift unimpeded downstream and develop in low-velocity lateral habitats. For example, three minnows with drift-dependent early life stages that are declining across much of the Interior Plains partly due to river fragmentation (Perkin and Gido 2011) occurred in at least nine sites within the Grand River system (Plains Minnow *Hybognathus placitus*, Shoal Chub *M. hyostoma*, Silver Chub *M. storeriana*).

Lower nestedness indicative of less dispersal limitation also contributed to lower beta diversity in the Grand River system. Supplemental habitats resembling large-river habitats in the Missouri River (e.g., fine substrates, high turbidity) predominated the Grand River system and may have facilitated dispersal by LRS species farther upstream. Although the farthest upstream sites in the Grand River revealed some evidence of dispersal limitation, nestedness was far higher in the Meramec River system. For example, upstream dispersal limitation in the Meramec River system was apparent by rkm 145 (reflected by high nestedness), and only 1–2 LRS species ranged upstream at or beyond rkm 184 where discharge was low ($37 \text{ m}^3/\text{s}$). Higher risks of stranding and predation in shallower upstream reaches (Schlosser 1987) or accumulating dispersal costs (Brönmark et al. 2014) could inhibit species from dispersing farther upstream in the Meramec River system. Moreover, the farthest upstream reaches in the Meramec River system could fail to attract species beyond middle reaches where potential complementary habitats already exist (e.g., large shoals with coarse substrates).

Underlying influence of dispersal on large-river specialist fish richness

We found positive relationships between LRS richness at sites within tributaries and discharge, which generally supports applications of SDRs to assess conservation value of tributaries for riverine fishes (e.g., Xenopoulos and Lodge 2006, Pracheil et al. 2013, Laub et al. 2018). However, high similarity of habitats throughout the Grand River and lower dispersal limitation likely resulted into more moderately sloped SDRs in the Grand River system than the Meramec River system. Thus, conservation plans that transcend physiographic boundaries (e.g., prairie vs. upland regions) may need to account for broadly differing habitats within tributaries by developing region- or river-specific SDRs.

Discharge imperfectly represented the influence dispersal from the Mississippi/Missouri rivers on LRS richness based on spatially structured mismatches between observed and SDR-predicted richness, especially in the Meramec River system. Mismatches arose near areas of network branching where sites were low

discharge, yet accessible to dispersing species from nearby Mississippi/Missouri River source populations. For example, Meramec River system SDRs underestimated richness in both tributary branches (by 2.3–8.7 spp.) and Meramec River sites between tributary-branch confluences (by 0.6–3.2 spp.), while overestimating richness at more isolated sites upstream (by 1.1–5.8 spp.). We suspect dispersal from the Missouri River also structured LRS richness in the Grand River system, but less dispersal limitation in upstream reaches meant LRS richness was similar throughout the Grand River system (8–17 spp.). Consequently, there was less residual variation in Grand River SDRs that could be explained by downstream distance to the Missouri River.

Failing to account for downstream connectivity and dispersal could impact decisions related to basinwide conservation planning and restoration. The area of reconnected habitat for migratory fishes is often a guiding criterion for prioritizing barrier removals (Kemp and O'Hanley 2010, Puijenbroek et al. 2019). If distributional patterns of LRS species in the Meramec River system are generalizable to other upland tributaries, discharge might underestimate important habitats for migratory species in tributary branches with high connectivity to migrant sources. One migratory species detected in the Meramec River system's lowermost tributary branch (Big River, rkm = 62) was Alabama Shad *Alosa alabamae*, an anadromous species that has been extirpated throughout the Ohio and upper Mississippi rivers following construction of semi- and impermeable barriers (Mettee and O'Neil 2003). Nine of twenty-one age-0 Alabama Shad collected in the Meramec River system were from the Big River (suggestive of spawning habitat), whereas none were collected in the Meramec River upstream of rkm 120 despite these sites having discharge comparable to Big River (see abundances by life stage in Appendix S1: Table S7). Given the wide-ranging life cycles of many LRS species, undervaluing downstream connectivity in tributaries could also impact other imperiled species (Galbraith et al. 2018). For example, at least 19 LRS species that we collected are known hosts for larval freshwater mussels in the Meramec River system, including Alabama Shad (INHS and OSUMBD 2017, see Hinck et al. [2012] for mussel list). Thus, prioritizing

conservation for LRS species within tributaries might mutually benefit multiple imperiled taxonomic groups.

Research assumptions, conclusions, and gaps

Our study revealed specific mechanisms underlying SDRs in nonwadeable tributaries, but it is important to recognize our study was limited to two river basins and 22 sites. Further, our comparative study also assumed the Grand and Meramec river systems broadly represented patterns within prairie and upland physiographic regions, respectively. Our sampling protocols were developed specifically to minimize false absences in nonwadeable rivers by pairing six complementary gears (Dunn and Paukert 2020). However, we likely failed to detect some LRS species. For example, we did not detect Paddlefish, but Paddlefish have been detected recently in both systems (Dunn et al. 2018, Tripp et al. 2019). Thus, it is important that our findings be corroborated within other nonwadeable tributaries. Such efforts will need to overcome logistical challenges that have traditionally hampered sampling nonwadeable rivers at riverscape scales (Thorpe 2014).

We found LRS fish richness within tributaries was structured by discharge, broad and fine-scale habitat availability, and downstream connectivity to Mississippi/Missouri rivers. The predictive strength of discharge likely resulted from its integration of a suite of longitudinal changes in habitat. Discharge, however, imperfectly accounted for downstream connectivity in reaches with high network branching. These findings indicate conservation practitioners may want to consider pairing spatial predictors with discharge in models explaining LRS species' distributions and diversity (Chaput-Bardy et al. 2017, Lin et al. 2017). For example, increasingly sophisticated spatial prioritization algorithms can weight connectivity in riverscape conservation plans, thereby preserving both corridors and critical habitat patches for migratory fishes (Hermoso et al. 2018, Linke et al. 2019).

There are several other factors that might impact the conservation value of tributaries for LRS fishes. Many of these factors are research gaps stemming from insufficient site-level data on the spatiotemporal availability of habitat and LRS fish distributions (Cooke et al. 2012).

Beyond mean annual discharge, other dimensions of flow, such as timing and duration, could impact tributary use (Laub et al. 2018). For example, temporally varying flows induce seasonal and annual variation in tributary use by at least some LRS species (Lyons et al. 2016, Dyer and Brewer 2020), and it is unclear how these dynamics affect LRS fish diversity patterns within tributaries through time. Moreover, little is known about which specific habitats within tributaries are important for several LRS fishes and whether these habitats are supplemental or complementary to habitats in mainstem large rivers (Galat and Zweimüller 2001). Synchrony between key dimensions of flow regime and availabilities of complementary habitats in tributaries is likely important for recruitment and survival of LRS fishes (Pracheil et al. 2009). Examining a broader suite of traits across more tributaries may provide insights into other functional drivers of tributary use. Addressing these research gaps will be important for prioritizing conservation actions within and among tributaries to conserve populations of riverine fishes.

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