CONSERVATION BIOGEOGRAPHY OF LOTIC FISHES IN THE MISSOURI AND COLORADO RIVER BASINS

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by
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ABSTRACT

To improve our understanding of lotic fish ecology and improve conservation efforts, I 1) identified potentially ecologically important tributaries (PEITs) and evaluated their effects on fish assemble structure, 2) evaluated factors affecting spatial transferability of species distribution models (SDMs), and 3) evaluated the drivers of non-native fish establishment in the Missouri and Colorado River basins (MRB and CRB). The effects of PEIT likely vary among rivers as all Missouri River PEITs affected fish assemblage structure, but only half of upper Colorado River basin PEITs affected fish assemblage structure. Species distribution models transferred from the MRB to the CRB for 15 of 25 species, but transferability was not predictable based on species characteristics, re-enforcing the hypothesis that transferability is species- and context-specific. Support for Human Activity, Biotic Resistance and Biotic Acceptance hypotheses as the drivers of non-native fish establishment varied by family, but these hypotheses rarely explained significant variability in the probability of non-native Salmonidae, Catostomidae, and Cyprinidae occurrence. These results may suggest that other factors (e.g., natural factors) drive non-native species distributions at the spatial (i.e., grain=stream segment; extents=physiographic divisions, and MRB and CRB combined) and taxonomic (i.e., family) scales considered in this study. This study aids conservations efforts by providing an efficient approach for identifying ecologically important tributaries and improving predictions of non-native species establishment.

CHAPTER 1- GENERAL INTRODUCTION

Introduction

Lotic ecosystems are in great need of conservation. Lotic ecosystems support high biodiversity of fish, invertebrates, plants, and algae, but also provide many human uses (e.g., food, navigation, power generation, drinking water, irrigation; Malmqvist and Rundle 2002). This human-dependency on lotic waters has resulted in lotic ecosystems becoming one of the most altered ecosystem classes in the world (Malmqvist and Rundle 2002) and freshwater species extinction rates similar to those of the most-impacted terrestrial ecosystem (i.e., tropical rainforest; Ricciardi and Rasmussen 1999).

Approximately 39% of freshwater fish species in North America are imperiled; representing a 92% increase since 1989 (Jelks et al. 2008). This trend will likely continue because the human population is predicted to increase from approximately 7.6 billion in 2017 to 11.2 billion in 2100 (UN 2017), and lotic fishes are expected to be impacted by future climate change (Abell 2002; Malmqvist and Rundle 2002).

Humans primarily affect lotic fishes through habitat alteration and species introductions (Malmqvist and Rundle 2002; Dudgeon et al. 2006). Habitat alteration was a causal factor in 73% of North American freshwater fish extinctions in the past century (Miller et al. 1989). Hydrological alteration (i.e., damming, channelization, and water removal) affects fish assemblages by inundating lotic habitats, modifying the timing and magnitude of stream flow, altering water temperatures, and increasing habitat fragmentation (Poff et al. 1997; Malmqvist and Rundle 2002; Roy et al. 2005). Meanwhile, land use changes affect water quality, substrate heterogeneity, water

temperature, physical habitat, and allochthonous energy inputs (Malmqvist and Rundle 2002; Diana et al. 2006; Moerke and Lamberti 2006; Wehrly et al. 2006). Non-native species contributed to 68% of North American fish extinctions (Miller et al. 1989) and affect native fishes through predation (e.g., Shelton et al. 2015; Ballew et al. 2016; Ellender et al. 2018), competition (e.g., Love et al. 2018), hybridization (e.g., Muhlfeld et al. 2017), and disease transmission (Malmqvist and Rundle 2002; Gozlan et al. 2010; Cucherousset and Olden 2011). The effects of non-native species on native fishes likely increased recently because the number of non-native fish species in the USA was estimated to increase from 69 (in 1990) to 150 by 2025 (Malmqvist and Rundle 2002).

The ability to predict non-native fish establishment is critical to the conservation of native lotic fishes. Potential management approaches for non-native species include no action, preventing establishment to new areas (e.g., preventing introductions of new species or containment of established species), population control to reduce non-native species impacts, and eradication (Britton et al. 2011). Of these, preventative measures are often the most cost-effective options (Wittenberg and Cock 2001), but knowledge of the factors that affect non-native species establishment is needed to effectively prevent their spread (Blanchet et al. 2009).

The "Human Activity", "Biotic Acceptance", and "Biotic Resistance" hypotheses are often used to predict non-native species establishment (Olden et al. 2010). The Human Activity Hypothesis suggests that non-native species establishment is best predicted by human activities that increase propagule pressure (i.e., the number of species introductions or number of individuals introduced) or habitat alteration (Olden et al. 2010). The Biotic Acceptance Hypothesis predicts environmental conditions affect native

and non-native species similarly, resulting in a positive relationship between native and non-native species richness (Fridley et al. 2007). Conversely, the Biotic Resistance Hypothesis predicts a negative relationship between native and non-native species richness because native species are expected to prevent non-native species establishment through competition and predation (Levine and D'Antonio 1999). Currently, the drivers of non-native species establishment in lotic ecosystems are uncertain, but resolving this information gap may help resource managers prevent future non-native species invasions.

An improved understanding of the ability of species distribution models (SDMs) to transfer between regions (i.e., spatial transferability) may also aid non-native species prevention efforts. Species distribution models predict areas where non-native species are likely to establish by applying a model developed in one area to an area of potential introduction (Olden and Jackson 2002; Peterson 2003), but accurate predictions rely on adequate transferability between regions (Randin et al. 2006; Wenger and Olden 2012; Huang and Frimpong 2016). Multiple biotic factors (e.g., ecological trait plasticity and species prevalence) were identified as potentially affecting SDM transferability (Elith and Leathwick 2009; Huang and Frimpong 2016), but it remains unclear if transferability of lotic fish SDMs is predictable based on species characteristics. The ability to predict if SDMs reliably transfer to new areas would allow resource managers to confidently implement non-native species prevention actions based on SDM predictions.

Although non-native species affect many lotic ecosystems, understanding the ability of tributaries to remediate the effects of hydrological alteration is especially important to the conservation of large river fishes. Many large rivers are impacted by impoundments (Hughes et al. 2005), but tributaries may reduce the effects of

impoundment because they are sources of the abiotic factors affected by impoundment (e.g., sediment, turbidity, streamflow, and water temperature; Malmqvist and Rundle 2002; Rice et al. 2008). Currently, however, there is a lack of information on which tributaries are likely ecologically important to mainstem rivers and if tributary effects can be generalized across geographic regions (Rice et al. 2008). Therefore, developing an approach to identify tributaries that likely affect abiotic characteristics of large rivers may lead to improved management of large rivers by providing a means to target tributaries for research and conservation efforts.

I had a unique opportunity to evaluate how biotic and abiotic factors affect fish distributions and assemblage structure in the Colorado and Missouri River Basins to improve our understanding of the ecology of lotic fishes and inform conservation efforts. Specifically, my goals were to improve our ability to predict the establishment of non-native species, and predict which tributaries are likely to be ecologically important and evaluate their effects on fish assemblage structure. To accomplish this goal, I conducted three independent studies:

Chapter 2- Identifying Potentially Ecologically Important Tributaries of Large Rivers and Their Effects on Small-Bodied Fish Assemblage Structure

Chapter 3- Transferability of Species Distribution Models of Lotic Fishes Across River Basins

Chapter 4- Family-Level Evaluation of the Drivers of Non-Native Lotic Fish Establishment

These studies were written as stand-alone manuscripts with co-authors for publication in peer-reviewed journals and, therefore, were written using the “we” pronoun and may contain redundant material.

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CHAPTER 2- IDENTIFYING POTENTIALLY ECOLOGICALLY IMPORTANT TRIBUTARIES OF LARGE RIVERS AND THEIR EFFECTS ON SMALL-BODIED FISH ASSEMBLAGE STRUCTURE

Abstract

Many large river ecosystems are impacted by hydrological alterations, and tributaries have gained attention for their potential to remediate the impacts of these alterations. However, it is unclear which tributaries are most likely to affect large river ecosystems. We identified potentially ecologically important tributaries (PEIT) of the Missouri, San Juan, upper Colorado, and Green Rivers (USA) as those tributaries that created discontinuities in longitudinal trends in landscape-level environmental data of these rivers (i.e., watershed area, dam storage density, and predominant surficial lithology) using *k*-means cluster analysis. We then compared small-bodied fish assemblage structure upstream and downstream of a subset (i.e., those with sufficient fish sampling data) of PEIT with discriminant analysis to evaluate if these PEIT were associated with changes in fish assemblage structure. We identified one PEIT for the middle Missouri River, three for the San Juan River, and four each for the lower Missouri, upper Colorado, and lower Green Rivers. Half of PEIT were identified by dam storage density or surficial lithology but not watershed area, and only one PEIT was identified by watershed area without also being identified by dam storage density or surficial lithology. All Missouri River PEIT evaluated affected fish assemblage structure, whereas only a subset of PEIT of the Colorado, Green, and San Juan Rivers affected fish assemblage structure, potentially due to low species richness in these rivers relative to the

Missouri River. The importance of watershed characteristics for identifying PEIT and the effects of tributaries on fish assemblages likely vary among rivers. Our approach for identifying PEIT may be used to identify tributaries for conservation and restoration actions, delineate ecologically relevant sampling reaches, and identify tributaries that likely have distinct chemical signatures for microchemistry studies.

Introduction

An improved understanding of the effects of tributaries on mainstem rivers is critical to the conservation of large river ecosystems (Rice et al. 2008). Many large river ecosystems are impacted by hydrological alterations (e.g., channel morphology alteration, flow regulation, and flow diversion), but tributaries may remediate the effects of mainstem alteration because they reintroduce abiotic elements of rivers that were lost or altered (e.g., sediment, stream flow, and water temperature; Galat et al. 2001; Malmqvist and Rundle 2002; Rice et al. 2008) and serve as surrogate mainstem habitat (Brown and Coon 1994; Tyus and Saunders 2001; Pracheil et al. 2013). Furthermore, tributary confluences are considered biodiversity hotspots due to increased habitat and biological diversity (Benda et al. 2004b; Fernandes et al. 2004; Kiffney et al. 2006; Rice et al. 2006; Rice et al. 2008).

The ecological effects of tributaries on mainstem rivers may depend on tributary watershed characteristics, but research is needed to identify which tributaries are likely ecologically important and improve our understanding of their effects on large river ecosystems. The Link Discontinuity Concept indicates that, at intermediate spatial scales (i.e., 1-100 km), a small number of tributaries provide sufficient streamflow and sediment to create discontinuities in the longitudinal pattern of hydrological and geomorphological

conditions of rivers and, ultimately, affect ecosystem structure or processes (Rice et al. 2001). These tributary inputs (i.e., streamflow and sediment) are ultimately driven by watershed characteristics (e.g., size, geology, soil characteristics, land use, hydroclimate, geomorphology, and vegetation; Hynes 1975; Rice et al. 2001; Sable and Wohl 2006; Charlton 2008), so understanding tributary effects on mainstem watershed characteristics may provide insight on the ecological effects of tributaries on large river ecosystems. The ecological effects of tributaries are also dependent on the degree of tributary impoundment because unimpounded tributaries likely provide more natural sediment, temperature, and flow regimes than impounded tributaries (Rice et al. 2008). Finally, the effects of tributaries on mainstem rivers may vary between different climatic regions, as Benda et al. (2004a) found that fewer tributaries in arid environments were geomorphically significant than tributaries in humid environments, potentially due to differences in disturbance regimes. Currently, however, our knowledge of the mechanisms responsible for tributary effects, the generality of tributary effects across rivers and regions, and our ability to predict which tributaries are most likely ecologically important within a river network is lacking (Rice et al. 2008). Addressing these information gaps would improve large river conservation efforts by allowing ecologically important tributaries to be efficiently identified and targeted for management actions.

To improve large river conservation efforts, the objectives of this study were to develop an approach for identifying potentially ecologically important tributaries (PEIT) based on watershed characteristics, evaluate the effects of these tributaries on small-bodied fish assemblage structure, and compare characteristics of PEIT and their effects on fish assemblage structure among diverse river basins. We used the Missouri,

Colorado, Green and San Juan Rivers to illustrate our approach across a range of river sizes, climate, and hydrological alteration.

Methods

Study Site

We focused on two reaches of the Missouri River: 1) the middle Missouri River from Fort Randall Dam, South Dakota [river km (rkm) 1,416] to Gavins Point Dam, Nebraska-South Dakota (rkm 1,305), and 2) the lower Missouri River (i.e., Gavins Point Dam to the confluence of the Mississippi River; Figure 2.1). The Missouri River basin is primarily (70% of basin area) composed of the semi-arid (32 cm mean annual precipitation), highly erodible Great Plains, but the lower Missouri River basin is composed of the more humid Central Lowlands (40-102 cm mean annual precipitation) and Ozark Plateau physiographic provinces (> 100 cm mean annual precipitation; Galat et al. 2005b). The Missouri River was historically a turbid, warmwater river characterized by a braided channel with numerous islands and sandbars, but impoundments and channelization have substantially altered habitat, sediment load, water temperature, flow regimes, and subsequently, fish populations (Galat et al. 2005a, 2005b). We delineated the Missouri River into two reaches to prevent mainstem impoundment (i.e., Gavins Point Dam) from confounding our results. The middle Missouri River has altered temperature, flow, and sediment regimes due to impoundment, and is composed of approximately 71 rkm of unchannelized river from Fort Randall Dam to the headwaters of Lewis and Clark Lake, Nebraska-South Dakota, and 40 rkm of reservoir (Galat et al. 2005b). The lower Missouri River has an altered flow regime due to upstream reservoirs and is unchannelized from Gavins Point Dam to Sioux City, Iowa (rkm 1,178), but is

channelized and leveed from Sioux City to the confluence with the Mississippi River (Galat et al. 2005a, 2005b). The Missouri River supports 136 fish species (106 native species), and species richness increases from the upper Missouri River (64 species) to the lower Missouri River (110 species; Galat et al. 2005a).

We also examined three river reaches in the upper Colorado River basin: 1) the Green River downstream of Flaming Gorge Dam, Wyoming (rkm 661) to its confluence with the Colorado River, 2) $\geq 7^{\text{th}}$ order (based on NHDPlus Version 1; USEPA 2005) reaches of the upper Colorado River (i.e., confluence of the Gunnison River to Glen Canyon Dam, Arizona), and 3) $\geq 7^{\text{th}}$ order reaches of the San Juan River (i.e., downstream of the Chaco River; rkm 357) located in Utah, New Mexico, Colorado, and Wyoming (Figure 2.1). The Colorado River basin is primarily semi-arid shrub lands and desert shrubs, and the large rivers of the basin flow primarily through highly erodible, sedimentary deposits (Blinn and Poff 2005). Mean annual precipitation in the upper Colorado River basin is 22 cm/yr, and most of the streamflow of the Green, upper Colorado, and San Juan Rivers originates as mountain snowmelt (Blinn and Poff 2005). These rivers were historically turbid, warmwater rivers, but, like the Missouri River, sediment, temperature, and flow regimes of the Green River are substantially influenced by a mainstem dam (i.e., Flaming Gorge Dam; Blinn and Poff 2005). Although the upper Colorado and San Juan Rivers are impounded, these dams impound smaller portions of the watershed (i.e., $\leq 8,400 \text{ km}^2$). In addition to habitat fragmentation and alteration caused by dams, these rivers have lost habitat diversity due to local channelization efforts associated with human development (Valdez and Muth 2005). Fish species richness is lower in the upper Colorado River basin than in the Missouri River basin; there are

approximately 65 species (14 native) in the entire upper Colorado River basin, with 37 species (12 native) in the Green River, and 26 species (7 native) in the San Juan River (Blinn and Poff 2005; Valdez and Muth 2005).

Identification of Potentially Ecologically Important Tributaries by Watershed

Characteristics

Consistent with the Link Discontinuity Concept (Rice et al. 2001), we identified potentially ecologically important tributaries (PEIT) as those tributaries that created discontinuities in the longitudinal profile of watershed characteristics of mainstem rivers. We evaluated longitudinal trends of watershed area, non-carbonate residual material surficial lithology (percent of watershed), and dam storage density (i.e., volume of water stored in reservoirs/watershed area) to represent tributary size, potential sediment inputs, and hydrological alteration, respectively. For each mainstem river, we quantified upstream watershed characteristics (dam storage density and surficial lithology) for each stream segment (NHDPlus Version 1; USEPA and USGS 2005) using the Catchment Attribute Allocation and Accumulation Tool (http://www.horizon-systems.com/nhdplus/NHDPlusV1_tools.php). Stream segments were typically lengths of stream extending between two confluences, but were shorter if side channels, divergences, or other features occurred (McKay et al. 2012). We acquired surficial lithology data from Cress et al. (2010) to represent surficial and bedrock geology characteristics that may affect sediment dynamics. We evaluated trends in non-carbonate residual material because it was the predominant surficial lithology class (i.e., greater percent of watershed than any other lithology class) for the middle and lower Missouri River, upper Colorado River, lower Green River, and the San Juan River. Non-carbonate residual material is

formed by the chemical and physical breakdown of non-carbonate (i.e., non-limestone or other carbonate rocks) bedrock such as sedimentary rock (Soller and Reheis 2004). Other common (> 5% watershed area) lithology types in the Missouri River basin included loamy glacial till, fine- and coarse-textured eolian sediment, and alluvium and fine-textured coastal zone sediment. Coarse-textured eolian sediment, silicic residual material, and alluvium and fine-textured coastal zone sediment were common lithology types in the upper Colorado River basin. We acquired dam storage data from the 2010 National Inventory of Dams database (USACE 2010) and remediated obvious errors in the dataset (e.g., duplicate records) prior to quantifying dam storage density. We acquired watershed area (km²) values from the NHDPlus database (USEPA and USGS 2005).

We used *k*-means cluster analysis to group stream segments of each river that had similar values separately for each watershed characteristic. Next, we arranged segments longitudinally from upstream to downstream and identified the tributaries that caused changes in group membership as PEIT. *K*-means cluster analysis groups samples into a pre-determined number of clusters (i.e., *k*) based on their Euclidian distances (i.e., straight-line distance; Kwak and Peterson 2007) using a variance-minimizing algorithm to minimize the distance within groups. To provide an unbiased means of determining the appropriate number of groups, we determined the optimal number of clusters by evaluating the relationship between model fit (i.e., R^2) and *k* (Kwak and Peterson 2007) and selected the value of *k* such that subsequent clusters did not improve R^2 by ≥ 0.05 . We fixed the random number seed to ensure replicability of our analyses and used the “nstart” option (nstart=25) in R software (R Core Team 2015) to find the optimum initial centroids because the *k*-means clustering procedure depends on initial centroid location

for each cluster (Tan et al. 2005). We calculated the ratio of tributary watershed characteristic to mainstem watershed characteristic immediately upstream of the confluence (i.e., “trib:US”) to illustrate how watershed characteristics of PEIT compared to the mainstem. A trib:US value near one indicated that the tributary and mainstem had similar values of the watershed characteristic, a value > 1 indicated that the tributary had a higher value of a watershed characteristic than the mainstem, and a value < 1 indicated that the tributary had a lower value of a watershed characteristic than the mainstem.

Effects of Potentially Ecologically Important Tributaries on Fish Assemblage Structure

We acquired small-bodied fish sampling data from the Upper Colorado River Endangered Fish Recovery Program (1990-2012) for the Colorado, Green, and San Juan Rivers, and the Pallid Sturgeon Population Assessment and Associated Fish Community Monitoring Program (2005-2013) for the Missouri River. These programs conduct standardized sampling during the summer and fall to collect age-0 and small-bodied fishes. The Upper Colorado River Endangered Fish Recovery Program sampled with seines (0.32 mm mesh, 4.6 m long, 1.2 m deep; USFWS 1987) in backwater areas, and the Pallid Sturgeon Population Assessment and Associated Fish Community Monitoring Program sampled shallow water (≤ 1.2 m) habitats with mini-fyke nets (3-mm ace mesh; Welker and Drobish 2016, Welker et al. 2016). We chose to evaluate the effects of tributaries on small-bodied and age-0 fishes to reduce the potential effects of migratory behavior (common to adult, large-bodied riverine species) on our analyses.

For each PEIT, we evaluated differences between the fish assemblage upstream of the confluence and the fish assemblage downstream of the confluence with discriminant analysis. Discriminant analysis identifies linear combinations of species-specific relative

abundance data that best discriminate between assemblages (i.e., discriminant functions) and provides discriminant function-variable (i.e., species) correlation scores that describe each species' influence in discriminating between assemblages (Kwak and Peterson 2007). We limited our analyses to fish samples that occurred within 5 rkm of PEIT confluences to reduce the potential of large-scale longitudinal changes in fish assemblage structure (Vannote et al. 1980; Galat et al. 2005a; Pegg and Pierce 2002b) obscuring the effects of tributaries that may occur if larger reaches were examined, while also being consistent with the scale of geomorphic effects of tributaries (Benda et al. 2004b). When multiple PEIT occurred within 5 rkm of each other (i.e., Sagers Wash and Dolores River in the upper Colorado River), sample reaches were delineated by the location of the adjacent PEIT to reduce confounding effects of multiple PEIT. Samples that occurred in mainstem river side channels near confluences (e.g., Niobrara River confluence) were excluded from the analysis if we were unable to determine based on aerial imagery and sampling location if they were upstream or downstream of the confluence. We limited our analysis to common species (i.e., present in $\geq 5\%$ of samples per confluence) because rare species are unlikely to affect fish community dynamics, but may obscure meaningful trends if included in analyses (Kwak and Peterson 2007). Fish data was summarized to catch per unit effort (CPUE) as fish per net (seine) or fish per net-night (mini-fyke net) and log transformed [i.e., $\log_{10}(\text{CPUE}+1)$] prior to analysis to improve normality. We used leave-one out cross validation to assess the accuracy of assemblage predictions (i.e., upstream or downstream of PEIT) from the discriminant analysis. We limited our evaluation of the effects of PEITs on fish assemblage structure to PEIT with at least 20 samples per assemblage (i.e., ≥ 20 samples from the upstream assemblage and ≥ 20

samples from the downstream assemblage; Kwak and Peterson 2007). Sample size requirements necessitated pooling samples across years, but 40-82% of samples were paired (upstream and downstream) within years for each confluence. For example, if 10 samples occurred upstream of the confluence and 5 samples occurred downstream of the confluence in a year, then 67% ($n=10/15$) of samples were paired within that year [i.e., (5 upstream samples + 5 downstream samples)/ 15 total samples].

Results

The middle Missouri River contained 75 stream segments, and the lower Missouri River contained 606 streams segments. Watershed area increased from $649.8 \times 10^3 \text{ km}^2$ at Fort Randall Dam to $686.4 \times 10^3 \text{ km}^2$ at Gavins Point Dam, and to $1,231.8 \times 10^3 \text{ km}^2$ at the confluence of the Mississippi River (Figure 2.2). Dam storage density decreased from $121.7 \times 10^3 \text{ m}^3/\text{km}^2$ at Fort Randall Dam to $115.7 \times 10^3 \text{ m}^3/\text{km}^2$ immediately upstream of Gavins Point Dam. Dam storage density decreased from $116.7 \times 10^3 \text{ m}^3/\text{km}^2$ at Gavins Point Dam to $104.9 \times 10^3 \text{ m}^3/\text{km}^2$ at the confluence of the Mississippi River, with a minimum of $95.4 \times 10^3 \text{ m}^3/\text{km}^2$ immediately upstream of the Osage River (Figure 2.2). Percent watershed non-carbonate surficial lithology decreased from 59.4 at Fort Randall Dam to 40.7 at the Mississippi River confluence, with a minimum of 40.3 immediately upstream of the Osage River (Figure 2.2).

The upper Colorado River had 352 stream segments. Watershed area increased from $43.4 \times 10^3 \text{ km}^2$ at the confluence of the Gunnison River to $275.7 \times 10^3 \text{ km}^2$ at Glen Canyon Dam (Figure 2.2). Dam storage density decreased from $105.0 \times 10^3 \text{ m}^3/\text{km}^2$ at the confluence of the Gunnison River to $55.1 \times 10^3 \text{ m}^3/\text{km}^2$ at Glen Canyon Dam. Percent non-

carbonate surficial lithology increased from 52.4 at the confluence of the Gunnison River to 73.4 at Glen Canyon Dam.

The lower Green River reach was composed of 472 stream segments. Watershed area increased from $38.4 \times 10^3 \text{ km}^2$ at Flaming Gorge Dam to $114.4 \times 10^3 \text{ km}^2$ at the confluence of the Colorado River (Figure 2.3). Dam storage density decreased from $137.4 \times 10^3 \text{ m}^3/\text{km}^2$ at Flaming Gorge Dam to $70.0 \times 10^3 \text{ m}^3/\text{km}^2$ at the confluence of the Colorado River. Percent watershed non-carbonate surficial lithology increased from 72.5 at Flaming Gorge Dam to 78.6 at the confluence of the Colorado River.

The San Juan River had 236 stream segments. Watershed area increased from $38.8 \times 10^3 \text{ km}^2$ at the confluence of the Chaco River to $62.9 \times 10^3 \text{ km}^2$ at the confluence of the Colorado River (Figure 2.3). Dam storage density decreased from $48.0 \times 10^3 \text{ m}^3/\text{km}^2$ at the confluence of the Chaco River to $26.4 \times 10^3 \text{ m}^3/\text{km}^2$ at the confluence of the Colorado River. Percent watershed non-carbonate surficial lithology decreased from 76.2 at the confluence of the Chaco River to 73.6 at the confluence of the Colorado River.

Identification of Potentially Ecologically Important Tributaries by Watershed

Characteristics

In the middle Missouri River, two clusters were identified for watershed area ($R^2=0.99$), surficial lithology ($R^2=0.99$), and dam storage density ($R^2=0.99$; Table 2.1; Figure 2.2). The Niobrara River was the only PEIT identified and created discontinuities in all three watershed characteristics. The Niobrara River increased watershed area from 645.3 to $683.9 \times 10^3 \text{ km}^2$, but decreased dam storage density from 120.9 to $116.1 \times 10^3 \text{ m}^3/\text{km}^2$ and non-carbonate surficial lithology from 59.0 to 57.5%.

Four PEIT were identified in the lower Missouri River. Two PEIT created discontinuities in watershed area ($k=3$; $R^2=0.97$), two created discontinuities in surficial lithology ($k=3$; $R^2=0.95$), and three created discontinuities in dam storage density ($k=3$; $R^2=0.90$; Table 2.1; Figure 2.2). The Big Sioux River was identified as a PEIT by dam storage density and decreased dam storage density from 108.6 to 106.0 $10^3 \text{ m}^3/\text{km}^2$ (Table 2.1). The Platte River was identified as a PEIT based on watershed area, dam storage density, and surficial lithology. The Platte River increased watershed area from 785.7 to 945.5 10^3 km^2 , and decreased dam storage density from 103.3 to 100.2 $10^3 \text{ m}^3/\text{km}^2$ and watershed non-carbonate surficial lithology from 50.0 to 46.5%. The Kansas River, identified by watershed area and surficial lithology, increased watershed area from 980.7 to 1,128.9 10^3 km^2 and decreased watershed non-carbonate surficial lithology from 45.1 to 41.2%. The Osage River was identified by dam storage density, and increased dam storage density from 95.4 to 106.1 $10^3 \text{ m}^3/\text{km}^2$.

Four PEIT were identified for the upper Colorado River: Sagers Wash, Dolores River, Green River, and San Juan River (Table 2.1; Figure 2.2). Two PEIT were identified by watershed area ($k=3$; $R^2=0.99$), two were identified by surficial lithology ($k=3$; $R^2=0.99$), and three were identified by dam storage density ($k=4$; $R^2=0.97$). Sagers Wash, identified by dam storage density, decreased dam storage density from 93.0 to 91.8 $10^3 \text{ m}^3/\text{km}^2$ (Table 2.1). The Dolores River was identified by surficial lithology, and increased watershed non-carbonate surficial lithology from 57.3 to 63.6%. The Green River was identified as a PEIT by watershed area, surficial lithology, and dam storage density. The Green River increased watershed area from 67.7 to 182.1 10^3 km^2 , increased non-carbonate surficial lithology from 63.9 to 73.2%, and decreased dam storage density

from 80.7 to 74.0 $10^3 \text{ m}^3/\text{km}^2$. The San Juan River, identified by watershed area and dam storage density, increased watershed area from 205.9 to 268.8 10^3 km^2 and decreased dam storage density from 65.7 to 56.5 $10^3 \text{ m}^3/\text{km}^2$.

We identified four PEIT for the Green River: Vermillion Creek, Yampa River, White River, and Willow Creek (Table 2.1; Figure 2.3). Two PEIT were identified by watershed area ($k=3$; $R^2=0.95$), one was identified by dam storage density ($k=2$; $R^2=0.93$), and two were identified by non-carbonate surficial lithology ($k=3$; $R^2=0.92$). Vermillion Creek and Willow Creek were identified as PEIT by surficial lithology. Vermillion Creek increased watershed non-carbonate surficial lithology from 73.3 to 74.5%, and Willow Creek increased watershed non-carbonate surficial lithology from 77.0 to 77.5% (Table 2.1). The Yampa River was identified as a PEIT by watershed area and dam storage density. The Yampa River increased watershed area from 43.1 to 64.3 10^3 km^2 , and decreased dam storage density from 122.9 to 86.5 $10^3 \text{ m}^3/\text{km}^2$. The White River was identified by watershed area and increased watershed area from 78.3 to 91.1 10^3 km^2 .

We identified three PEIT for the San Juan River: Mancos River, Montezuma Creek, and Chinle Creek (Table 2.1; Figure 2.3). One PEIT was identified by watershed area ($k=2$; $R^2=0.93$), two PEIT were identified by dam storage density ($k=3$; $R^2=0.97$), and three PEIT were identified by non-carbonate surficial lithology ($k=3$; $R^2=0.98$). The Mancos River was identified as a PEIT by dam storage density and non-carbonate surficial lithology. The Mancos River increased non-carbonate surficial lithology from 76.9 to 78.0% and decreased dam storage density from 44.8 to 42.7 $10^3 \text{ m}^3/\text{km}^2$. Montezuma Creek, identified by surficial lithology, decreased non-carbonate surficial lithology from 77.8 to 76.5%. Chinle Creek was identified as a PEIT by watershed area,

surficial lithology, and dam storage density. Chinle Creek increased watershed area from 47.0 to 57.0 10^3 km^2 , decreased non-carbonate surficial lithology from 75.8 to 73.8%, and decreased dam storage density from 35.3 to 29.1 $10^3 \text{ m}^3/\text{km}^2$.

Across mainstem rivers, eight (50%) tributaries were identified as PEIT based on watershed area. Seven of these tributaries were also identified by surficial lithology or dam storage density. Most PEIT identified by watershed area were $\geq 15\%$ the size of the mainstem (i.e., $\text{trib:US} \geq 0.15$; Table 2.1). However, the Niobrara River was identified by watershed area with a tributary: mainstem size ratio of 0.05 for the relatively short middle Missouri River. Tributaries identified as PEIT by surficial lithology or dam storage density but not watershed area typically had watershed area $\leq 7\%$ of the mainstem (i.e., $\text{trib:US} \leq 0.07$; Table 2.1). The Dolores River (Colorado River PEIT) was not identified by watershed area despite having greater relative watershed area ($\text{trib:US}=0.24$) than two PEIT identified by watershed area in the upper Colorado River basin [i.e., White River (Green River PEIT) $\text{trib:US}=0.16$; Chinle Creek (San Juan River PEIT) $\text{trib:US}=0.21$; Table 2.1].

Eight PEIT were identified by surficial lithology or dam storage density but not by watershed area. These PEIT had surficial lithology or dam storage densities that differed considerably from the mainstem river. The five PEIT (all upper Colorado River basin) identified by lithology but not watershed area had watersheds 3-24% the size of the mainstem (i.e., $\text{trib:US}=0.03\text{-}0.24$; Table 2.1) but had considerably different non-carbonate lithology than the mainstem. Montezuma Creek (59.2%) had lower non-carbonate surficial lithology than the San Juan River (77.8%; $\text{trib:US}=0.76$), but the other tributaries had higher non-carbonate surficial lithology than the mainstem ($\text{trib:US} \geq$

1.25; Table 2.1). Four PEIT were identified by dam storage density but not watershed area. These tributaries were small compared to the mainstem (trib:US watershed area $\leq$ 0.06) and typically had lower dam storage density than the mainstem (i.e., trib:US dam storage density $\leq$ 0.15; Table 2.1). However, dam storage density of the Osage River was 4.5 times greater than that the mainstem Missouri River (i.e., trib:US dam storage density=4.5; Table 2.1).

Effects of Potentially Ecologically Important Tributaries on Fish Assemblage Structure

We evaluated the effects of PEIT on fish assemblage structure for three Missouri River tributaries: Niobrara River (n=110 mini-fyke net samples), Platte River (n=50 mini-fyke samples) and Osage River (n=57 mini-fyke net samples). We did not evaluate the effects of the Big Sioux or Kansas Rivers (n=26 mini-fyke net samples each) because there was insufficient fish sampling data adjacent to these confluences. We evaluated the effects of PEIT on fish assemblage structure for two Colorado River tributaries: Sagers Wash (n=68 seine samples) and the Dolores River (n=61 seine samples). We did not evaluate the effects of the Green (n=0 seine samples downstream of confluence) or San Juan Rivers (n=0 seine samples). We evaluated the effects of the White River (n=137 seine samples) on fish assemblage structure of the Green River but did not evaluate the effects of Vermillion Creek (n=0 seine samples), the Yampa River (n=0 seine samples), or Willow Creek (n=2 seine samples upstream of confluence). We evaluated the effects of the Mancos River (n=61 seine samples), Montezuma Creek (n=119 seine samples), and Chinle Creek (n=112 seine samples) on fish assemblage structure of the San Juan River.

A total of 45 species were caught in the Missouri River within 5 rkm of the Niobrara River confluence (Table 2.2). All 26 species that occurred in $\geq 5\%$ of samples were caught downstream of the confluence, but 4 species (Orangespotted Sunfish *Lepomis humilis*, Freshwater Drum *Aplodinotus grunniens*, Flathead Catfish *Pylodictis olivaris*, and Bigmouth Buffalo *Ictiobus cyprinellus*) were not caught upstream of the Niobrara River. Thirty-seven species were caught in the lower Missouri River within 5 rkm the Platte River confluence, and 22 species occurred in $\geq 5\%$ of samples (Table 2.2). All common species (i.e., occurred in $\geq 5\%$ of samples) were caught downstream of the confluence, but Orangespotted Sunfish and White Crappie *Pomoxis annularis* were not caught upstream of the Platte River. Thirty species were caught in the lower Missouri River within 5 rkm of the Osage River confluence. Of the 22 common species caught, 3 (Brook Silverside *Labidesthes sicculus*, Mimic Shiner *Notropis volucellus*, and Spotted Bass *Micropterus punctulatus*) were not caught upstream of the confluence, and 1 species (Common Carp *Cyprinus carpio*) was not caught downstream of the confluence.

Sixteen species were caught in the Colorado River adjacent to the Sagers Wash (9 common species) and Dolores River confluences (10 common species; Table 2.2). Thirteen species, including seven common species, were caught in the Green River adjacent to the White River confluence (Table 2.2). Ten species were caught in the San Juan River adjacent to the Mancos River (3 common species) and Montezuma Creek (6 common species) confluences, and nine species were caught within 5 rkm of the Chinle Creek confluence (4 common species; Table 2.2). All common species were caught upstream and downstream of each confluence.

All Missouri River PEITs affected fish assemblage structure, but only half of upper Colorado River basin PEIT affected fish assemblage structure. In the Missouri River, fish assemblages upstream of the Niobrara ($p=0.008$), Platte ($p=0.019$), and Osage ($p=0.001$) Rivers differed from assemblages immediately downstream of these tributaries. Predictability of fish assemblages (i.e., upstream or downstream of PEIT) was better than random (i.e., > 50% correct prediction rate) for the Niobrara (68% accurate prediction rate), Platte (74% accurate prediction rate), and Osage (77% accurate prediction rate) Rivers. The proportion of variance in fish assemblage structure explained by the discriminant analysis (i.e., squared canonical correlation) was highest for the Osage River (0.67), followed by the Platte River (0.65), and the Niobrara River (0.39).

In the upper Colorado River Basin, the White River ($p=0.041$) affected fish assemblage structure of the Green River, but Sagers Wash ($p=0.086$; 59% accurate prediction rate) and Dolores River ($p=0.091$; 56% accurate prediction rate) did not affect fish assemblage structure of the Colorado River. Chinle Creek ($p=0.030$) and Montezuma Creek ($p < 0.001$) affected fish assemblage structure of the San Juan River, but the Mancos River did not ($p=0.710$). Assemblage predictability was better than random for the White River (60% accurate prediction rate), Chinle Creek (56% accurate prediction rate), and Montezuma Creek (60% accurate prediction rate). The proportion of variance in fish assemblage structure explained by discriminant analysis was lower for upper Colorado River basin PEIT than for Missouri River PEIT: Montezuma Creek=0.18, White River=0.10, and Chinle Creek=0.09.

In the Missouri River, more species were associated with the downstream assemblage than the upstream assemblage for the Niobrara ($n=18$ of 26; 69%) and Platte

River (n=12 of 22; 55%) confluences based on discriminant analysis, but more species were associated with the upstream assemblage for the Osage River confluence (n=12 of 22; 55%; Figure 2.4). In the Green River, most species (n=5 of 8; 62%) were associated with the assemblage upstream of the White River confluence (Figure 2.5). For the San Juan River, more species (n=3 of 4; 75%) were associated with the assemblage upstream of the Chinle Creek confluence than downstream of the confluence; whereas an equal number of species (n=3 of 6; 50%) were associated with the reaches immediately upstream and downstream of the Montezuma Creek confluence (Figure 2.5).

Of the 14 species that occurred at all three Missouri River confluences, four species (Emerald Shiner *Notropis atherinoides*, Orangespotted Sunfish, Red Shiner *Cyprinella lutrensis*, and White Crappie) were associated with the downstream assemblage of all three confluences, while zero species were associated with the upstream assemblage of all three confluences. Of the remaining ten species, discrepancies across tributaries were primarily due to species associations of the Osage River differing from those of the Platte and Niobrara Rivers (n=6; i.e., Black Crappie *Pomoxis nigromaculatus*, Bluegill *Lepomis macrochirus*, Common Carp, River Carpsucker *Carpiodes carpio*, Shortnose Gar *Lepisosteus platostomus*, and White Bass *Morone chrysops*; Figure 2.4). Of the four species that occurred at both San Juan River confluences, two were representative of upstream assemblages (i.e., Flannelmouth Sucker *Catostomus latipinnis* and Speckled Dace *Rhinichthys osculus*), while two species were inconsistent among confluences (i.e., Channel Catfish *Ictalurus punctatus* and Red Shiner; Figure 2.5).

Species representative of the Missouri River fish assemblage upstream of the Niobrara River were mostly cool, clear water species: Rock Bass *Ambloplites rupestris*, Smallmouth Bass *Micropterus dolomieu*, Bluntnose Minnow *Pimephales notatus*, and Walleye *Sander vitreus* (Figure 2.4). Common Carp, Orangespotted Sunfish, and Bigmouth Buffalo were most representative of the assemblage downstream of the Niobrara River (Figure 2.4). The most representative species of the fish assemblage upstream of the Platte River were Green Sunfish *Lepomis cyanellus*, Largemouth Bass *Micropterus salmoides*, and Silver Chub *Macrhybopsis storeriana*, whereas Sand Shiner *Notropis stramineus*, White Bass, and Orangespotted Sunfish best characterized the assemblage downstream of the Platte River (Figure 2.4). Freshwater Drum, Common Carp, and Longnose Gar *Lepisosteus osseus* best described the fish assemblage upstream of the Osage River, while Emerald Shiner, Bluegill, and Mimic Shiner were most indicative of the assemblage downstream of the Osage River (Figure 2.4).

Sand Shiner, Bluehead Sucker *Catostomus discobolus*, and Common Carp were the species most representative of the Green River fish assemblage upstream of the White River, while Black Crappie and Colorado Pikeminnow *Ptychocheilus lucius* were the most representative species of the assemblage downstream of the confluence (Figure 2.5). Speckled Dace and Channel Catfish were most representative of the San Juan River fish assemblage upstream of Montezuma Creek, whereas Fathead Minnow *Pimephales promelas*, Bluehead Sucker, and Red Shiner were most representative of the assemblage downstream of the confluence (Figure 2.5). Finally, Flannelmouth Sucker, Red Shiner, and Speckled Dace were most representative of the San Juan River fish assemblage

upstream of Chinle Creek, while Channel Catfish was most representative of the assemblage downstream of the confluence (Figure 2.5).

Discussion

Our study found that watershed characteristics such as surficial lithology and dam storage density, in addition to watershed area, were valuable for identifying tributaries that may affect large river ecosystems. Tributary size is a logical metric for identifying PEIT because it is a primary driver of geomorphic effects at confluences (Rhoads 1987; Benda et al. 2004a, 2004b) and predicts tributaries that function as surrogate mainstem habitat (Pracheil et al. 2013), but half of the PEIT identified in this study were not identified by tributary size (i.e., watershed area). Rather, surficial lithology or dam storage density of PEIT that were not identified by watershed area differed enough from the mainstem to create discontinuities in the longitudinal profile of these characteristics. Additionally, only one PEIT was identified solely by watershed area. This suggests that most large tributaries are often associated with changes in the watershed characteristics (e.g., lithology and impoundment) that determine the tributary inputs (i.e., volume and characteristics of water and sediment) responsible for geomorphological changes at confluences (Vogel et al. 1999; Rice et al. 2001). Consideration of watershed characteristics may also provide valuable insight into the mechanisms responsible for the ecological effects of tributaries on mainstem rivers. For example, the Niobrara River likely reduces the effects of mainstem impoundment on temperature and flow regimes because it is relatively unimpounded compared to the mainstem, but it may not restore some aspects of the sediment regime (e.g., suspended sediment) because it decreased watershed non-carbonate surficial lithology. Rather, the Niobrara River increased

watershed coarse eolian (mostly sand) surficial lithology and has substantially affected physical habitat in the middle Missouri River by contributing to a large, braided delta upstream of Lewis and Clark Lake (Galat et al. 2005a; Elliot and Jacobson 2006). Conversely, the Osage River increased mainstem dam storage density, suggesting that some tributaries may increase mainstem habitat alteration (e.g., altered temperature, flow, or sediment regimes).

The relative importance of a particular watershed characteristic for identifying PEIT likely differs among mainstem rivers. Half of the Green River PEITs and all three San Juan River PEITs were identified by lithology, but their effects on mainstem non-carbonate surficial lithology were minor ($\leq 2\%$ change in non-carbonate surficial lithology) and may not be ecologically meaningful. In contrast, Missouri River and Colorado River PEIT identified by surficial lithology created notable discontinuities in the longitudinal profile (1.5-9.2% change in non-carbonate surficial lithology) and may be more likely to affect mainstem sediment dynamics, physical habitat, and turbidity. Meanwhile, all PEIT identified by dam storage density in our study created obvious discontinuities in the longitudinal profile of dam storage density that may be ecologically meaningful. Except for the Osage River, these tributaries reduced dam storage density and, therefore, may reduce the effects of hydrological alteration on the mainstem.

Numerous large tributaries and tributaries identified as ecologically important in other studies were not identified as PEIT in this study, potentially due to our cutoff for identifying PEIT (i.e., improve $R^2 \geq 0.05$) and their locations within the river basin (e.g., proximity to dams or other tributaries). First, three tributaries of the Green River (i.e., Duchesne, Price and San Rafael Rivers) provide habitat for endangered large river fishes

(Tyus and Saunders 2001; Bottcher et al. 2013) but were not identified as PEIT in this study. Second, two Missouri River tributaries, the Grand ($20.4 \times 10^3 \text{ km}^2$; 0.02 size ratio) and James ($47.9 \times 10^3 \text{ km}^2$; 0.07 size ratio) Rivers, were not identified as PEIT but had larger watersheds than the Big Sioux River (i.e., PEIT identified by dam storage density; $18.5 \times 10^3 \text{ km}^2$; 0.02 size ratio). The James River caused visible changes in the three landscape factors (rkm=1,261; Figure 2.2), but we suspect it was not identified as a PEIT because few stream segments ($n=11$; 23 rkm) occurred between Gavins Point Dam and the James River confluence. Meanwhile, the Grand River was likely not identified as a PEIT because it enters the Missouri River near its confluence with the Mississippi River (approximately rkm 394), where few tributaries are likely of sufficient size to affect a river of this size. Third, the Duchesne River (Green River rkm 401; watershed area= $9.9 \times 10^3 \text{ km}^2$; 0.14 size ratio) was not identified as a PEIT despite visibly increasing dam storage density, and the White River was not identified as a PEIT by dam storage density despite being large (i.e., identified as PEIT by watershed area) and having substantially different dam storage density than the mainstem Green River. These phenomena (Duchesne River not identified as a PEIT and the White River not identified by dam storage density) were likely a result of these confluences being located approximately 3 rkm (6 stream segments) apart. In this scenario, the Duchesne River increased dam storage density, but this increase was almost immediately reduced by the White River. Ultimately, the omission of these tributaries from our identification of PEIT was likely, in part, due to our cutoff for identifying PEIT (i.e., improve R^2 by ≥ 0.05), and we recommend reducing this threshold (e.g., improve R^2 by ≥ 0.01) in future research that aims to maximize the number of PEIT identified. These results suggest that it may be

unwarranted to infer that tributaries that were not identified as PEIT in our study lack ecological importance and highlight that our approach is just one of potentially numerous tools for identifying ecologically important tributaries.

Our study suggests that PEIT more consistently affected small-bodied fish assemblages of the Missouri River than PEIT of the large rivers in the upper Colorado River basin, potentially due to differences in species assemblages between mainstem rivers. All three Missouri River PEIT that we evaluated affected fish assemblage structure, but only three of the six upper Colorado River basin PEIT that we evaluated affected fish assemblage structure. Furthermore, accuracy of assemblage predictions was consistently higher for assemblages adjacent to Missouri River PEIT ($\geq 68\%$) than for assemblages adjacent to upper Colorado River basin PEIT ($\leq 60\%$). Species richness was considerably higher in the middle and lower Missouri River ($n=22-26$ common species adjacent to PEIT confluences) than in the large rivers of the upper Colorado River basin ($n=3-10$ common species adjacent to PEIT confluences). Therefore, our analyses had more potential variables (i.e., species) to use to discriminate between assemblages for the Missouri River compared to the rivers in the upper Colorado River basin. The hypothesis that tributary effects on fish assemblage structure were more easily determined for the Missouri River due to the high species richness is consistent with Baltz et al. (1987) and Capone and Kushlan (1991), who found that discriminant function prediction accuracy increased when more predictor variables were used. Finally, accuracy rates in this study were lower than other studies that used discriminant analysis to evaluate differences in fish assemblages (e.g., $> 80\%$ accuracy; Rodríguez and Lewis Jr. 1997; Gido et al. 2000;

Herlihy et al. 2006), potentially due to the close proximity of assemblages (i.e., adjacent stream reaches) and the lack of physical barriers between assemblages.

Tributary effects on small-bodied fish assemblage structure likely vary among tributaries, in part, due to differences in mainstem channel morphology. The middle Missouri River is unchannelized, and the Niobrara River affected physical habitat (Galat et al. 2005a; Elliot and Jacobson 2006) and small-bodied fish assemblage structure. The lower Missouri River, however, is highly modified (e.g., channelization, levees, and engineered confluences) resulting in a self-dredging channel (Jacobson and Galat 2006) that likely reduces tributary effects on physical habitat of the lower Missouri River. Therefore, tributaries of the lower Missouri River may have a greater impact on fish assemblage structure due to their effects on streamflow and temperature regimes rather than their effects on physical habitat. A similar situation may exist (i.e., lack of tributary impacts on physical habitat) in the upper Colorado River basin because some reaches of these rivers are high gradient, canyon bound or highly incised (Blinn and Poff 2005) and likely have high capacity to transport tributary sediment.

Hydrological characteristics may result in seasonal effects of tributaries on fish assemblages that vary among tributaries. Tributary effects on mainstem river habitat depend on the quantity and characteristics of the water and sediment the tributary provides (Rice et al. 2001), but these inputs vary seasonally. Streams in the upper Colorado River basin are primarily fed by mountain run-off and, therefore, have flow regimes characterized by high spring flows and low summer flows (Blinn and Poff 2005). These peak spring flows are likely important for spawning adults, whereas summer base flows affect juvenile nursery habitat (Tyus and Saunders 2001). As a result, it is possible

upper Colorado River basin tributaries did not consistently affect small-bodied fish assemblage structure during summer (evaluated here) due to reduced tributary inputs but have significant ecological effects during spring for adults (e.g., increased water temperature and food availability, resting and feeding areas; Tyus and Karp 1990). Conversely, in the Missouri River basin, the Platte and Niobrara Rivers have significant base-flow resulting from groundwater inputs (Galat et al. 2005b) and, as a result, may have more consistent seasonal effects on total streamflow, water temperature, physical habitat, and fish assemblage structure than tributaries with less base-flow.

Identifying the potential mechanisms responsible for tributary effects on fish assemblage structure is difficult because tributaries often affected multiple watershed characteristics simultaneously, but our approach to identifying PEIT provided some insight into potential mechanisms. The Niobrara and Platte Rivers were identified as PEIT by size, lithology, and dam storage so the mechanisms responsible for differences in fish assemblage structure could be a combination of changes in water temperature, turbidity, physical habitat, or flow characteristics. However, the effects of the Platte River on fish due to changes in physical habitat may be limited by channel engineering to reduce sedimentation in the channelized lower Missouri River. Meanwhile, the Osage River increased mainstem dam storage density, and some species associations were consistent with increased hydrological alteration downstream of the confluence. Freshwater Drum (among other species) were characteristic of the upstream assemblage, while Spotted Bass, Black Crappie, and Emerald Shiner were characteristic of the downstream assemblage. Unaltered, lotic environments may provide energetic benefits for Freshwater Drum, while habitats impacted by impoundment may be more

energetically favorable for Black Crappie and Spotted Bass because Rypel and Bayne (2009) found that Freshwater Drum growth and lipid content was higher in lotic habitats than lentic habitats, but Black Crappie and Spotted Bass had higher lipid content (both species) and growth (Spotted Bass only) in lentic habitats. Furthermore, our observation that Emerald Shiners were associated with increased hydrologic alteration downstream of the Osage River was consistent with Bailey and Allum (1962), who indicated that Emerald Shiners were rare in the Missouri River prior to impoundment but have likely increased since impoundment. Finally, speculation of the mechanisms associated with PEIT effects on fish assemblage structure in the Colorado River basin is unwarranted given the low predictive performance of our discriminant analysis (i.e., prediction accuracy rates $\leq 60\%$; proportion of variance explained ≤ 0.18) for these tributaries.

Conservation Implications

Tributaries serve multiple ecologically important roles across spatial scales. At the watershed scale, tributaries modify the longitudinal trends in stream ecosystem structure and function proposed by the River Continuum Concept (Vannote et al. 1980; Bruns et al. 1984; Minshall et al. 1985). At intermediate spatial scales, a limited number of tributaries contribute sufficient streamflow and sediment to mainstem rivers to cause considerable shifts in hydrological and geomorphological conditions, and ultimately biotic assemblage composition of rivers (i.e., Link Discontinuity Concept; Rice et al. 2001). Consistent with the Link Discontinuity Concept, we found that a few tributaries created discontinuities in landscape-level environmental data and small-bodied fish assemblage structure, but the effects varied among tributaries. Finally, tributaries provide habitat for (Tyus and Saunders 2001; Bottcher et al. 2013; Pracheil et al. 2013) and affect

recruitment (e.g., Pracheil et al. 2009) of large river fishes, and create localized areas of increased habitat and biological diversity (Benda et al. 2004b; Fernandes et al. 2004; Kiffney et al. 2006; Rice et al. 2006; Rice et al. 2008) at finer spatial scales.

Our evaluation of longitudinal trends in watershed characteristics was an efficient approach for identifying PEIT. First, the sizes of tributaries identified as PEIT with our approach (0.01-1.69 tributary: mainstem watershed ratio) were consistent with the sizes of tributaries identified as geomorphically significant by Benda et al. (2004a; typically 0.007 to 0.06 tributary: mainstem watershed ratio). Second, numerous PEIT affected fish assemblage structure in this study or were identified as ecologically important in other studies. In the middle Missouri River, the Niobrara River affects physical habitat by creating a braided delta (Elliot and Jacobson 2006), Paddlefish *Polyodon spathula* recruitment (Pracheil et al. 2009), and small-bodied fish assemblage structure (this study). Additionally, Pegg and Pierce (2002a) suggested that lower Missouri River tributaries (e.g., Osage and Kansas Rivers) ameliorate the effects of impoundment on streamflow variability parameters (e.g., flow per unit area, coefficient of variation of annual flow, flow predictability, flow contingency) based on stream gage data, but did not explicitly evaluate the effects of these tributaries. Conversely, our results suggest that the Osage River increases hydrological alteration of the Missouri River based on watershed dam storage density. Finally, the White and Yampa Rivers (Green River PEITs) were identified as the tributaries of greatest importance to endangered fish recovery in the Green River basin (Tyus and Saunders 2001) and were used to delineate reaches when developing flow and temperature recommendations (Muth et al. 2000).

Our approach for identifying PEIT may be useful for targeting tributaries for restoration or protection, delineating ecologically relevant sampling reaches, and guiding microchemistry studies. Our results suggest that the Osage River could be targeted for restoration because it increased hydrological alteration (i.e., dam storage density) of the Missouri River. Conversely, the Niobrara, Big Sioux, Platte, and Kansas Rivers could be prioritized for protection against future hydrological alteration because they likely reduce the effects of mainstem Missouri River impoundment. Our approach could also be used to delineate ecologically relevant sampling reaches because sampling units defined by hydrology, geomorphology, or factors that drive riverine productivity (e.g., floodplain connectivity and degree of impoundment) are expected to be particularly valuable for advancing our understanding of large river ecology (Bayley 1995; Johnson et al. 1995). In this context, treatment and control sites for research studies could be selected from within the same landscape factor cluster (i.e., between two PEIT) to minimize environmental variability among sites. Finally, hard-part (i.e., otolith and fin ray) microchemistry is a popular tool for determining environmental history and stock assignment of fishes, but habitats need different water chemistry signatures for this tool to be effective (Pracheil et al. 2014). Water chemistry in riverine ecosystems is primarily driven by watershed characteristics (Douglas 1968; Hynes 1975). For example, Phelps et al. (2012) and Wuellner et al. (2017) indicated that differences in microchemistry among rivers were likely due to differences in watershed geology. Therefore, our approach for identifying PEIT using landscape-scale environmental data may also be used to identify tributaries that likely have distinct water chemistry characteristics or alter mainstem water chemistry.

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Tables

Table 2.1. Potentially ecologically important tributaries (PEIT) identified by watershed area, dam storage density, or non-carbonate surficial lithology for the Missouri, upper Colorado, Green, and San Juan Rivers. River km (Rkm) of confluences based on NHD stream network, and Colorado River values represent distance upstream of Glen Canyon Dam, AZ. Bold typeface indicates values of characteristics that resulted in PEIT. Watershed characteristic values presented for the mainstem upstream (US) and downstream (DS) of confluence, tributary (Trib), and tributary/upstream of the confluence (Trib:US).

River	Tributary	Rkm	Watershed characteristic	Watershed characteristic											
				Watershed area (1,000 km ²)				Non-carbonate surficial lithology (%)				Dam storage density (1,000 m ³ /km ²)			
				US	DS	Trib	Trib: US	US	DS	Trib	Trib: US	US	DS	Trib	Trib: US
Middle Missouri River	Niobrara River	1,340	Area, dam storage, lithology	654.3	683.9	29.6	0.05	59.0	57.5	23.8	0.40	120.9	116.1	11.3	0.1
Lower Missouri River	Big Sioux River	1,163	Dam storage	743.2	761.8	18.6	0.02	52.9	51.6	0.0	0.00	108.6	106.0	1.9	0.02
	Platte River	941	Area, dam storage, lithology	785.7	945.5	159.8	0.20	50.0	46.5	29.5	0.59	103.3	100.2	85.2	0.82
	Kansas River	579	Area, lithology	980.7	1,128.9	148.2	0.15	45.1	41.2	15.5	0.34	97.5	97.7	99.1	1.02
	Osage River	204	Dam storage	1,177.8	1,216.6	38.8	0.03	40.3	40.9	60.0	1.49	95.4	106.1	430.3	4.51
Colorado River	Sagers Wash	456	Dam storage	49.1	49.8	0.6	0.01	57.0	57.3	83.0	1.46	93.0	91.8	0.0	0.00
	Dolores River	452	Lithology	49.8	61.8	12.0	0.24	57.3	63.6	90.0	1.57	91.8	88.2	73.3	0.80
	Green River	295	Area, dam storage, lithology	67.7	182.1	114.4	1.69	63.9	73.2	78.6	1.23	80.7	74.0	70.0	0.87
	San Juan River	80	Area, dam storage	205.9	268.8	62.9	0.31	73.2	73.3	73.7	1.01	65.7	56.5	26.4	0.40

River	Tributary	Rkm	Watershed characteristic	Watershed characteristic											
				Watershed area (1,000 km ²)				Non-carbonate surficial lithology (%)				Dam storage density (1,000 m ³ /km ²)			
				US	DS	Trib	Trib: US	US	DS	Trib	Trib: US	US	DS	Trib	Trib: US
Green River	Vermillion Creek	592	Lithology	40.0	42.6	2.5	0.06	73.3	74.5	93.3	1.27	132.3	124.5	0.4	0.00
	Yampa River	558	Area, dam storage	43.1	64.3	21.2	0.49	74.7	76.2	79.3	1.06	122.9	86.5	12.4	0.10
	White River	398	Area, lithology	78.3	91.1	12.8	0.16	74.9	76.8	89.0	1.19	97.6	84.7	6.0	0.06
	Willow Creek	387	Lithology	92.0	94.5	2.4	0.03	77.0	77.5	98.3	1.28	83.9	81.8	0.0	0.00
San Juan River	Mancos River	307	Dam storage, lithology	35.1	37.2	2.1	0.06	76.9	78.0	95.9	1.25	44.8	42.7	6.5	0.15
	Montezuma Creek	251	Lithology	40.6	43.6	3.0	0.07	77.8	76.5	59.2	0.76	40.0	37.4	2.2	0.05
	Chinle Creek	208	Area, dam storage, lithology	47.0	57.0	10.0	0.21	75.8	73.8	64.1	0.85	35.3	29.1	0.0	0.00

Table 2.2. Percent of samples that each fish species occurred within 5 river km of potentially ecologically important tributary confluences in the Missouri (from 2005 to 2013), upper Colorado, Green, and San Juan Rivers (from 1990 to 2012). Bold typeface indicates species that occurred in $\geq 5\%$ of samples and were used in discriminant analyses.

Common name	Scientific name	Missouri River			Colorado River		Green River	San Juan River		
		Niobrara River	Platte River	Osage River	Sagers Wash	Dolores River	White River	Mancos River	Montezuma Creek	Chinle Creek
Bigmouth Buffalo	<i>Ictiobus cyprinellus</i>	9.1	4.0							
Bigmouth Shiner	<i>Notropis dorsalis</i>	0.9								
Black Bullhead	<i>Ameiurus melas</i>	1.8				3.3	1.5	3.3		
Black Crappie	<i>Pomoxis nigromaculatus</i>	20.0	10.0	10.5			14.6			
Bluegill	<i>Lepomis macrochirus</i>	30.0	50.0	22.8						
Bluehead Sucker	<i>Catostomus discobolus</i>				16.2	14.8	8.8	1.6	7.6	2.7
Bluntnose Minnow	<i>Pimephales notatus</i>	30.0		14.0						
Bonytail Chub	<i>Gila elegans</i>									
Brassy Minnow	<i>Hybognathus hankinsoni</i>	2.7								
Brook Silverside	<i>Labidesthes sicculus</i>		26.0	5.3						
Bullhead Minnow	<i>Pimephales vigilax</i>			35.1						
Burbot	<i>Lota lota</i>	0.9								
Channel Catfish	<i>Ictalurus punctatus</i>	14.5	50.0	28.1	2.9		0.7	50.8	57.1	61.6
Colorado Pikeminnow	<i>Ptychocheilus lucius</i>				4.4	8.2	14.6	1.6	3.4	0.9
Common Carp	<i>Cyprinus carpio</i>	21.8	10.0	7.0	7.4	8.2	13.1		0.8	
Creek Chub	<i>Semotilus atromaculatus</i>	1.8	2.0							
Emerald Shiner	<i>Notropis atherinoides</i>	35.5	68.0	38.6						
Fathead Minnow	<i>Pimephales promelas</i>	3.6	26.0	1.8	57.4	57.4	28.5	4.9	17.6	2.7
Flannelmouth Sucker	<i>Catostomus latipinnis</i>				7.4	9.8	4.4	4.9	25.2	6.3

Common name	Scientific name	Missouri River			Colorado River		Green River	San Juan River		
		Niobrara River	Platte River	Osage River	Sagers Wash	Dolores River	White River	Mancos River	Montezuma Creek	Chinle Creek
Flathead Catfish	<i>Pylodictis olivaris</i>	5.5	2.0	3.5						
Flathead Chub	<i>Platygobio gracilis</i>	0.9								
Freshwater Drum	<i>Aplodinotus grunniens</i>	7.3	62.0	52.6						
Gizzard Shad	<i>Dorosoma cepedianum</i>	11.8	54.0	29.8						
Goldeye	<i>Hiodon alosoides</i>			3.5						
Goldfish	<i>Carassius auratus</i>		2.0							
Grass Carp	<i>Ctenopharyngodon idella</i>		2.0	1.8						
Grass Pickerel	<i>Esox americanus vermiculatus</i>	4.5								
Green Sunfish	<i>Lepomis cyanellus</i>	17.3	22.0	7.0	2.9	9.8	4.4			
Humpback Chub	<i>Gila cypha</i>									
Johnny Darter	<i>Etheostoma nigrum</i>	13.6								
Largemouth Bass	<i>Micropterus salmoides</i>	19.1	10.0		4.4	4.9				
Longnose Gar	<i>Lepisosteus osseus</i>		16.0	21.1						
Mimic Shiner	<i>Notropis volucellus</i>			7.0						
Northern Pike	<i>Esox lucius</i>	4.5								
Orangespotted Sunfish	<i>Lepomis humilis</i>	9.1	12.0	12.3						
Plains Killifish	<i>Fundulus zebrinus</i>				10.3	13.1			3.4	0.9
Plains Minnow	<i>Hybognathus placitus</i>	0.9	2.0							
Plains Topminnow	<i>Fundulus sciadicus</i>		2.0							
Pumpkinseed	<i>Lepomis gibbosus</i>	0.9								

Common name	Scientific name	Missouri River			Colorado River		Green River	San Juan River		
		Niobrara River	Platte River	Osage River	Sagers Wash	Dolores River	White River	Mancos River	Montezuma Creek	Chinle Creek
Quillback	<i>Carpiodes cyprinus</i>	0.9	2.0							
Rainbow Smelt	<i>Osmerus mordax</i>	0.9		1.8						
Razorback Sucker	<i>Xyrauchen texanus</i>				1.5	1.6				
Red Shiner	<i>Cyprinella lutrensis</i>	20.0	76.0	61.4	58.8	57.4	38.0	41.0	52.1	41.1
Redside Shiner	<i>Richardsonius balteatus</i>									
River Carpsucker	<i>Carpiodes carpio</i>	26.4	14.0	8.8						
River Shiner	<i>Notropis blennius</i>		78.0	3.5						
Rock Bass	<i>Ambloplites rupestris</i>	10.0								
Roundtail Chub	<i>Gila robusta</i>				2.9	1.6				
Sand Shiner	<i>Notropis stramineus</i>	24.5	36.0		42.6	52.5	29.9			
Sauger	<i>Sander canadense</i>	4.5		3.5						
Shoal Chub	<i>Macrhybopsis aestivalis</i>		2.0	3.5						
Shorthead Redhorse	<i>Moxostoma macrolepidotum</i>	8.2	2.0							
Shortnose Gar	<i>Lepisosteus platostomus</i>	34.5	36.0	33.3						
Sicklefin Chub	<i>Macrhybopsis meeki</i>		2.0							
Silver Chub	<i>Macrhybopsis storeriana</i>	2.7	60.0	7.0						
Smallmouth Bass	<i>Micropterus dolomieu</i>	40.0	4.0							
Smallmouth Buffalo	<i>Ictiobus bubalus</i>	1.8	54.0							
Speckled Dace	<i>Rhinichthys osculus</i>				7.4	3.3	2.2	50.8	62.2	34.8
Spotfin Shiner	<i>Cyprinella spiloptera</i>	69.1	4.0							

Common name	Scientific name	Missouri River			Colorado River		Green River	San Juan River		
		Niobrara River	Platte River	Osage River	Sagers Wash	Dolores River	White River	Mancos River	Montezuma Creek	Chinle Creek
Spottail Shiner	<i>Notropis hudsonius</i>	14.5								
Spotted Bass	<i>Micropterus punctulatus</i>			5.3						
Stonecat	<i>Noturus flavus</i>	0.9								
Walleye	<i>Sander vitreus</i>	6.4	2.0							
Western Mosquitofish	<i>Gambusia affinis</i>		4.0	10.5	7.4	3.3		3.3	4.2	0.9
Western Silvery Minnow	<i>Hybognathus argyritis</i>	0.9								
White Bass	<i>Morone chrysops</i>	10.9	52.0	19.3						
White Crappie	<i>Pomoxis annularis</i>	15.5	6.0	12.3						
White Sucker	<i>Catostomus commersonii</i>				4.4	8.2	0.7			
Yellow Bullhead	<i>Ameiurus natalis</i>							1.6		
Yellow Perch	<i>Perca flavescens</i>	3.6								

Figures

Figure 2.1. Middle and lower Missouri River (right), and upper Colorado, Green, and San Juan Rivers (left) and subset of their tributaries. FRD=Fort Randall Dam, SD; GPD=Gavins Point Dam, NE-SD; FGD=Flaming Gorge Dam, UT; GCD=Glen Canyon Dam, AZ. Asterisks (*) indicate potentially ecologically important tributaries identified in this study, black dots (●) represent mainstem dams.

Figure 2.2. Longitudinal profile of watershed characteristics of the Missouri River downstream of Fort Randall Dam, SD (left) and the Colorado River from the Gunnison River to Glen Canyon Dam, AZ. Dotted lines indicate locations of potentially ecologically important tributaries. Dashed line represents location of Gavins Point Dam, NE-SD. Rkm=river kilometer. Letter designations (“A” – “E”) represent cluster designations from *k*-means clustering analysis. Values of rkm based on NHD stream network.

Figure 2.3. Longitudinal profile of watershed characteristics of the Green River downstream of Flaming Gorge Dam, UT (left), and the San Juan River downstream of the Chaco River (right). Dotted lines indicate locations of potentially ecologically important tributaries. Rkm=river kilometer. Letter designations (“A” – “C”) represent cluster designations from *k*-means clustering analysis. Values of rkm based on NHD stream network.

Figure 2.4. Discriminant analysis variable correlation scores for differentiating assemblages upstream (negative) and downstream (positive) of potentially ecologically important Missouri River tributaries: Niobrara (top), Platte (middle), and Osage Rivers (bottom).

Figure 2.5. Discriminant analysis variable correlation scores for differentiating assemblages upstream (negative) and downstream (positive) of potentially ecologically important tributaries of the Green (i.e., White River; top) and San Juan Rivers [i.e., Montezuma Creek (middle), and Chinle Creek (bottom)].

CHAPTER 3- TRANSFERABILITY OF SPECIES DISTRIBUTION MODELS OF LOTIC FISHES ACROSS RIVER BASINS

Abstract

Species distribution models (SDMs) are commonly applied to new areas to predict non-native fish species establishment and target areas for prevention measures. Currently, however, it is unclear if the ability of SDMs to effectively transfer to new areas (i.e., transferability) is predictable based on species characteristics. Therefore, we quantified transferability of fish SDMs from the Missouri River basin (MRB) to the Colorado River basin (CRB) for 25 species, evaluated the effects of species characteristics (i.e., family, nativity, temperature and substrate preference, reproductive guild, and trophic feeding guild) on SDM transferability, and compared SDMs among basins to examine patterns in SDM transferability. We developed SDMs for fishes occurring in 1st to 4th order streams using multivariate adaptive regression splines, landscape-level environmental data, and recent (1990-2012) fish sampling records. Species distribution models developed for MRB data had reasonable transferability to the CRB [area under the receiver operator curve (AUC) ≥ 0.7] for 15 of 25 species. Family, CRB nativity, temperature and substrate preferences, reproductive guild and trophic feeding guild were not significant predictors of transferability (i.e., AUC; $p=0.65$) but there was evidence of greater transferability for species with more specialized feeding strategies than generalist feeding strategies when we limited our analysis to groups with at least three species (one-way ANOVA $p=0.02$). Species distribution models developed for the MRB that transferred effectively to the CRB generally contained variables that

explained more variability (i.e., greater delta deviance) in CRB SDMs than those that did not transfer effectively. Transferability was generally not predictable based on species characteristics, re-enforcing the hypothesis that transferability is species- and context-specific. This finding highlights the need to use caution when transferring SDMs temporally or spatially, and the need to evaluate transferability when interpreting SDM predictions related to species introductions and climate change.

Introduction

Understanding the factors that affect the ability of species distribution models (SDMs) to transfer in time and space (i.e., transferability) is important for predicting the effects of climate change on species distributions and potential distributions of non-native species. Species distribution models describe relationships between environmental data and species occurrence or abundance (Elith and Leathwick 2009) and can be valuable tools for predicting changes in distributions due to climate change and potential non-native species invasions (Olden and Jackson 2002; Peterson 2003; Guisan and Thuiller 2005). However, evaluating model transferability is a particularly important component of model evaluation when SDMs are to be projected to new datasets (e.g., in time or space) because the utility of these predictions depends on adequate transferability (Randin et al. 2006; Wenger and Olden 2012; Huang and Frimpong 2016).

Transferability of SDMs is particularly important for informing conservation efforts of lotic fishes threatened by non-native species. Non-native species have negatively affected native fish assemblages, including contributing to the extinction of 27 species in North America (Miller et al. 1989), and their effects on native species have likely increased in the USA in recent years because non-native fish species richness was

predicted to double from 1990 to 2025 (Malmqvist and Rundle 2002). Management actions that prevent non-native species establishment are typically the most cost-effective options for managing the effects of non-native species (Wittenberg and Cock 2001), and transferring SDMs to new areas can identify areas of potential non-native fish establishment that can be targeted for prevention measures.

Despite the importance of SDM transferability to freshwater fish conservation and recent emphasis on SDM transferability (Wenger and Olden 2012; Huang and Frimpong 2016), the factors affecting transferability of lotic fish SDMs are relatively unclear. Yates et al. (2018) indicated that determining whether transferability was trait- or taxon-specific was one of the fundamental conceptual challenges in the study of ecological model transferability and, if addressed, could improve confidence in predictions from ecological models. Furthermore, multiple biotic factors were identified as potentially affecting SDM transferability in other taxa (e.g., ecological traits and trait plasticity, the equilibrium status of the species with its environment, prevalence of the species, and changes in biotic interactions over time or space; Elith and Leathwick 2009; Soininen and Luoto 2014; Huang and Frimpong 2016), but the effects of species characteristics (e.g., taxonomy and traits) on SDM transferability have not been examined thoroughly for lotic fishes.

To improve our understanding of lotic fish SDM transferability, we quantified transferability of fish distribution models from two adjacent but distinct basins in North America: the Missouri River basin (MRB) to the Colorado River basin (CRB). We also evaluated the effects of a variety of species characteristics on SDM transferability, and compared SDMs among basins to explain patterns in transferability of SDMs.

Methods

Study Site

The MRB and CRB provided an ideal opportunity to evaluate spatial transferability of SDMs because many non-native species in the CRB are native to the MRB and, therefore, evaluating the ability of SDMs developed for the MRB to transfer to the CRB simulates a typical application of spatially transferring SDMs to predict non-native species distributions. The CRB drains approximately 642,000 km² in the southwestern USA and northwestern Mexico and is composed primarily of semi-arid shrub lands and desert shrubs (Carlson and Muth 1989; Blinn and Poff 2005). There are 36 fish species (including 3 marine or brackish species and 23 endemic species) native to the CRB (Carlson and Muth 1989), but there are approximately 50 non-native species in the upper CRB (Valdez and Muth 2005) and 80 non-native species in the lower CRB (Mueller et al. 2005). The MRB drains approximately 1,371,017 km² in the USA and 25,100 km² in Canada and is primarily composed of the semi-arid (32 cm mean annual precipitation), highly erodible Great Plains (Galat et al. 2005). There are 138 native fish species and 35 non-native fish species in the MRB (Galat et al. 2005).

Fish Distribution Data

We summarized geo-referenced fish occurrence data for small streams (1st – 4th order) in the CRB (n=2,830 segments) and MRB (n=3,789 segments) collected between 1990 and 2012. Occurrence data was a compilation of state and federal agency databases, university and museum collections, and gray literature originally compiled by Annis et al. (2010), Whittier et al. (2011), and Whittier and Sievert (2014). Fish samples were linked to National Hydrography Dataset (NHDPlus version 1; USEPA and USGS 2005) stream

segments using a spatial join in ArcGIS (ESRI 2009). Stream segments are typically lengths of stream extending between two confluences, but may be shorter if side channels, divergences, or other features occur (McKay et al. 2012). Fish samples were summarized to species presence-absence for each stream segment because effort and gear types varied among data sources and sampling locations. Samples that did not capture any fish were excluded from our analysis. It was unclear if samples were single-species collections or community collections, but two or more species were documented at most stream segments (71.5%).

Environmental Data

We acquired and summarized natural and anthropogenic landscape-level environmental data to serve as predictor variables in SDMs. Many of these predictor variables were or were similar to factors found to affect fish distributions in the CRB and MRB in previous studies (Annis et al. 2010; Strecker et al. 2011; Whitney et al. 2017) and were readily available for the MRB and CRB (Table 3.1). Landscape-level factors were quantified for the stream segment, local catchment (“local”), and upstream network watershed (“network”) spatial scales. Natural environmental variables were stream order, base-flow index (percent of streamflow from groundwater), mean annual flow, mean annual velocity, slope, elevation, temperature, precipitation, and surficial lithology. Except for surficial lithology, these datasets were summarized by the data source. We quantified three network-scale surficial lithology (Cress et al. 2010) metrics for each stream segment using the Catchment Attribute Allocation and Accumulation Tool (http://www.horizon-systems.com/nhdplus/NHDPlusV1_tools.php) that represented the dominant lithology types that occur in both the MRB and CRB: percent non-carbonate

lithology, percent silicic lithology, and percent alluvium and fine-textured coastal zone sediment (Table 3.1). Local catchment and network watershed anthropogenic variables included in models were cultivated crop and urban land uses, number of dams, and population density (Esselman et al. 2011a; Table 3.1). We combined low, medium, and high intensity urban land uses into a total urban land use value.

We identified correlated landscape variables using Spearman's correlation analysis and removed variables that were strongly correlated ($r_s \geq |0.8|$) with other variables to reduce the effect of collinearity on our analyses (Huang and Frimpong 2016; Whitney et al. 2017). If a metric type (e.g., crop land use) was strongly correlated between spatial scales (e.g., local and network), then we retained the largest spatial scale (e.g., network) for analysis. Mean annual air temperature was highly correlated with elevation ($r_s = -0.81$, $p < 0.0001$), minimum air temperature ($r_s = 0.99$, $p < 0.0001$), and maximum air temperature ($r_s = 0.99$, $p < 0.0001$), and thus these three variables were removed from further analyses. Local catchment crop land use ($r_s = 0.86$, $p < 0.0001$), urban land use ($r_s = 0.82$, $p < 0.0001$), and population density ($r_s = 0.91$, $p < 0.0001$) were removed from the analysis because they were highly correlated with their network watershed counterparts.

Data Analysis

We developed species distribution models for 25 species that occur both in the CRB and MRB as a function of landscape-level environmental factors (Table 3.1) using multivariate adaptive regression splines (MARS) in program R version 3.4.2 (R Core Team 2017). Models were developed using the 'earth' package and incorporated modifications for binomial response variables (Milborrow 2017). We chose this modeling

approach because MARS models performed well in previous studies in the CRB (Strecker et al. 2011; Whitney et al. 2017), handle non-linear relationships that are common in ecological data, and can be readily transferred to new datasets (Leathwick et al. 2006). We limited our analysis to species that occurred at $\geq 3\%$ of MRB segments because SDMs created with fewer occurrences performed poorly (Whitney et al. 2017). We created SDMs based on MRB data to evaluate transferability because most species (n=17 of 25) that occurred in both basins were native to the MRB and non-native to the CRB. Therefore, this approach best represented the application of SDM transferability for predicting non-native species distributions. Finally, we created SDMs based on CRB data to verify that the environmental variables used adequately explained species distributions in the CRB and to enable comparison of SDMs among basins.

Model performance (MRB and CRB models) and transferability of the MRB models to the CRB was quantified using the area-under the receiver-operating curve (AUC), which measures the ability of the model to discriminate between species presence and absence sites (Elith et al. 2006), and is commonly used to evaluate SDM fit (e.g., Olden and Jackson 2002; Buisson et al. 2008; Strecker et al. 2011; Whitney et al. 2017) and transferability of SDMs (Randin et al. 2006; Vanreusel et al. 2007; Sundblad et al. 2009; Wenger and Olden 2012; Huang and Frimpong 2016; Iturbide et al. 2018). Area under the curve values range from 0 to 1; values < 0.5 indicate predictive ability is worse than random, values from 0.5 to 0.7 indicate poor model performance (i.e., only slightly better than random), values from 0.7 to 0.9 indicate reasonable performance, and values > 0.9 indicate models with very good ability to discriminate between presence and absence

sites (Pearce and Ferrier 2000). We considered MRB SDMs with $AUC \geq 0.7$ when applied to CRB data as models with reasonable transferability.

For each species, we quantified transferability (i.e., AUC) of the MRB SDM to: 1) all stream segments in the CRB with fish records, and 2) a subset of stream segments in the CRB with fish records located within ecological drainage units (EDUs; groups of USGS 8-digit hydrologic units with similar fish assemblages; Sowa et al. 2007) acquired from Esselman et al. (2011b) where the species occurred to reduce the potential effects of introduction history (i.e., lack of species introductions) on model transferability. Next, we evaluated how species characteristics affected transferability to all CRB stream segments using an analysis of variance (ANOVA), which was similar to the approach used by Soininen and Luoto (2014) and Huang et al. (2016) to evaluate the effects of species characteristics on SDM transferability. Given the lack of information on which species characteristics likely affect lotic fish SDM transferability (but see Huang et al. 2016), we evaluated the effects of a variety of species characteristics on transferability: family, CRB nativity, substrate and temperature preference, reproductive guild and trophic feeding guild. We acquired reproductive guild, feeding guild, and temperature and substrate preferences from Olden et al. (2006) for most species, and the remainder from Becker (1983), Brown (1971), Pflieger (1997), and Frimpong and Angermeier (2009) for Lake Chub *Couesius plumbeus* and Johnny Darter *Etheostoma nigrum*. We conducted a global ANOVA (all species and characteristics) and characteristic-specific one-way ANOVAs limited to treatment groups with at least three species to remove potential effects of groups with small sample size on the analyses. We considered characteristic-specific

differences significant at $\alpha=0.01$ (i.e., 0.05/5 comparisons) following Bonferroni correction for multiple comparisons.

We compared MRB SDMs to CRB SDMs for each species to examine if patterns in transferability were explained by similarities and differences in SDMs. We hypothesized that transferability would be higher for MRB SDMs with high variable overlap with CRB SDMs and those that contained the most important variables in CRB SDMs. We quantified the importance of predictor variables in SDMs using delta deviance, which is the change in model fit when a predictor variable is removed (Whitney et al. 2017). Delta deviance is scaled from 0 (variable not included in model) to 100 (most important variable). We then quantified four metrics for comparison between species whose models transferred (i.e., $AUC \geq 0.7$) and those whose models did not transfer ($AUC < 0.7$): 1) variable overlap, calculated as the percent of variables from CRB SDMs that were included in MRB SDMs; 2) number of MRB SDMs that contained the most-important CRB SDM variable; 3) CRB SDM importance of variables that occurred in SDMs from both basins for a species; and 4) CRB SDM importance of variables that only occurred in CRB SDMs. Consistent with Whitney et al (2017), we also evaluated if variable importance was correlated among basins for each species with Spearman correlation ($\alpha=0.05/25 = 0.002$, following Bonferroni correction for multiple comparison); variables that were omitted from SDMs received a variable importance value of zero. Finally, when the most important variable was consistent among basins, we graphically compared the effects of that variable on the probability of species occurrence to evaluate if the effect of this variable was consistent among basins.

Results

Transferability of Species Distribution Models Across Basins

For all species, SDMs created for the MRB had good predictive performance ($AUC > 0.8$; Table 3.2) in the MRB. These models had reasonable transferability to the CRB ($AUC \geq 0.7$) for 15 of 25 species (Table 3.2). The AUC was lowest for Channel Catfish *Ictalurus punctatus* and Mountain Sucker *Catostomus platyrhynchus* ($AUC=0.59$ and 0.61 , respectively), and was highest for Lake Chub, Yellow Bullhead *Ameiurus natalis*, and Western Mosquitofish *Gambusia affinis* ($AUC=0.87$, 0.88 and 0.93 , respectively). Limiting our analysis of transferability to stream segments within EDUs where the species occurred rarely improved transferability ($n=7$ of 25 species), and only increased AUC by ≥ 0.05 for three species (Table 3.2).

Species distribution models had AUC values > 0.7 for 59% of species that were non-native to the CRB, 67% of species native to the CRB, 60% of cold water species, 63% of cool water species, and 58% of warm water species (Table 3.3). Missouri River SDMs transferred to the CRB for 45% of species that prefer rubble substrate, up to 100% of species that prefer sand substrate ($n=2$). The SDMs transferred for 100% of piscivores ($n=1$) and invertivores ($n=7$), but only 50% ($n=5$) of invertivore/piscivores and 33% ($n=2$) of omnivores (Table 3.3). Transferability was lowest for Catostomidae (33% of species) and highest for Cottidae, Gasterosteidae, Percidae, and Poeciliidae species (100%; $n=1$ each; Table 3.3).

Family, CRB nativity, temperature and substrate preferences, reproductive guild and trophic feeding guild were not significant predictors of model transferability (i.e., AUC) from the MRB to CRB ($p=0.65$ for the global model). Additionally, one-way

ANOVAs indicated that temperature and substrate preferences, nativity, reproductive guild, and family did not affect transferability when the analysis was limited to groups with at least three species ($p > 0.6$). Mean AUC ranged from 0.72 for native species to 0.75 for non-native species, and from 0.68 for Catostomidae to 0.93 for Poeciliidae (Table 3.3). Mean AUC ranged from 0.73 for cold water species to 0.75 for warm water species, and from 0.72 for species that prefer rubble substrate to 0.85 for those that prefer sand. Mean AUC was highest for the external bearer (0.93; $n=1$) reproductive guild, followed by guarder, nest-spawner (0.75; $n=10$), non-guarder, brood hiders (0.73; $n=5$), and non-guarder, open substrate spawners (0.73; $n=9$). There was evidence of higher transferability for invertivores (mean=0.81) than omnivores (mean=0.70) and invertivore/piscivores (mean=0.73; Table 3.3), but this relationship was not statistically significant ($p=0.02$) following the Bonferroni correction.

Species Distribution Model Comparison Among Basins

All CRB SDMs had reasonable model fit ($AUC > 0.7$), and all but one SDM (i.e., Golden Shiner *Notemigonus crysoleucas*) had an $AUC > 0.8$ (Table 3.2). Across species, the most important variables driving species distributions were generally consistent between the MRB and CRB. Mean annual air temperature, mean annual precipitation, and base-flow index occurred in most SDMs (≥ 15 species in each basin) and had relatively high variable importance (i.e., delta deviance) across species when they occurred in SDMs (e.g., ≥ 40 ; Figure 3.1; Table 3.4). Network urban land use occurred in more SDMs in the MRB ($n=18$) than the CRB ($n=4$; Figure 3.1). Network crop land use, population density, and mean annual flow were more important in CRB SDMs (delta deviance > 60) than in MRB SDMs (delta deviance < 40 ; Figure 3.1).

Variable overlap between CRB and MRB SDMs was higher for species whose SDMs did not transfer (mean=71.0% of CRB SDM variables included in MRB SDMs) than those whose SDMs transferred (mean=66.3%; Figure 3.2). Missouri River Basin SDMs included all of the variables in CRB SDMs for two species whose SDMs did not transfer (i.e., Channel Catfish and Bluegill *Lepomis macrochirus*) and zero species whose SDMs transferred (Figure 3.2). Missouri River Basin SDMs included the most important variable (i.e., delta deviance=100) from CRB SDMs for 23 of the 25 species; this variable was omitted for one species whose SDM transferred (Brown Trout *Salmo trutta*; Figure 3.3), and one species whose SDM did not transfer (Mountain Sucker; Figure 3.4).

Missouri River basin SDMs that transferred well generally contained variables that were more important in CRB SDMs than those that did not transfer. Delta deviance of variables that occurred in SDMs for both basins was higher for species whose SDMs transferred (CRB average=59.8; Figure 3.2) than those that did not transfer (CRB average=53.4). Similarly, delta deviance of variables in CRB SDMs that were omitted from MRB SDMs was slightly higher for species whose models did not transfer (average=43.0) than for species whose SDMs transferred (average=39.2). Delta deviance was correlated between basins for two species whose SDMs transferred from the MRB to CRB [White Sucker *Catostomus commersonii* ($r_s=0.78$; $p < 0.001$) and Cutthroat Trout *Oncorhynchus clarkii* ($r_s=0.81$; $p < 0.001$; Figure 3.3)], but was not correlated between basins for any species whose SDMs did not transfer (Figure 3.4). Summaries of SDM delta deviance by species characteristics and basin are presented in Appendices 3.1-3.6.

The most important variable (mean annual air temperature) was consistent among basins for eight species (Table 3.4); five whose models transferred (Yellow Bullhead,

Red Shiner *Cyprinella lutrensis*, Western Mosquitofish, Green Sunfish *Lepomis cyanellus*, and Cutthroat Trout), and three whose models did not transfer (Bluegill, Golden Shiner, and Brook Trout *Salvelinus fontinalis*). The effects of mean annual air temperature on probability of occurrence were generally consistent across basins for species whose models transferred, but were less consistent for species whose models did not transfer. The probability of Cutthroat Trout occurrence was greatest at the coldest temperatures and decreased at warmer temperatures (Figure 3.5). In both basins, the probability of occurrence generally increased with temperature for Yellow Bullhead, Red Shiner, and Western Mosquitofish (Figure 3.5). However, probability of occurrence decreased with increasing temperature over a portion of the temperature range for Yellow Bullhead and Red Shiner in the MRB, and fluctuated over a portion of the temperature range for Western Mosquitofish in the CRB. The effect of temperature on the distribution of Green Sunfish was consistent among basins (i.e., probability of occurrence increased with temperature to a maximum, then decreased with increased temperature), but probability of occurrence peaked at different temperatures among basins (MRB=7.9°C; CRB=17.2°C). Probability of Bluegill occurrence increased with temperature up to approximately 7.8°C and then decreased with increased temperature in the MRB, but temperature had little effect on probability of Bluegill occurrence in the CRB. Similarly, Golden Shiner probability of occurrence increased with temperature in the MRB, but temperature had little effect on Golden Shiner occurrence in the CRB. In the CRB, the probability of Brook Trout occurrence was highest from -1.7 to 0.7°C, and then decreased with increasing temperature. In the MRB, the probability of Brook Trout

occurrence increased with temperature from -1.7 to 2.7°C, and then decreased as temperature increased.

Discussion

We found that SDMs based on landscape-level environmental factors transferred spatially across large river basins for 60% of the species evaluated. This percentage of successful transfers was higher than that observed by Huang and Frimpong (2016; 42-48%) for 144 combinations of species-basin transfers (21 species, 5 river basins) across the USA and was lower than that observed by Huang et al. (2016), who found that SDMs transferred temporally within the New River Basin, USA for 81% of species using a less conservative transferability threshold (AUC=0.6). However, only 54% (n=7 of 13) of the species in Huang et al. (2016) had at least one SDM that met our transferability threshold. Alternatively, 96% (n=24/25) of SDMs in our study met the $AUC \geq 0.6$ threshold used by Huang and Frimpong (2016) and Huang et al. (2016). These differences in percentage of successful SDM transfers between studies is likely, in part, due to the limited number of species that were consistent between studies, different transferability thresholds, and differences in modeling approaches between studies (Wenger and Olden 2012; Huang and Frimpong 2016).

Consistency of SDM transferability between studies varied by species, but our ability to compare transferability results to other studies was limited to a few species (n=6 of the 25 species we evaluated). Like Wenger and Olden (2012), our Brown Trout SDMs had higher transferability than our Brook Trout SDM. Transferability of Creek Chub *Semotilus atromaculatus* SDMs was consistent (i.e., low: $AUC < 0.7$) between our study and Huang and Frimpong (2016). Transferability of our Yellow Bullhead SDM was

higher (AUC=0.88) than SDMs in Huang and Frimpong (2016; AUC < 0.7).

Transferability was consistent between our study (spatial transferability) and Huang et al. (2016; temporal transferability) for Rainbow Trout *Oncorhynchus mykiss* (i.e., low, AUC < 0.7), but was inconsistent between studies for Brook Trout (i.e., low in our study) and Largemouth Bass *Micropterus salmoides* (i.e., high in our study). Finally, Brown Trout SDM transferability was high in our study, but was only high for one of the four model types in Huang et al. (2016). These differences in transferability for individual species between studies suggest that transferability may be context-specific (e.g., vary among geographic regions or between temporal and spatial transferability studies).

Transferability of lotic fish SDMs was generally not predictable based on species characteristics. Family, nativity, and traits did not explain patterns in transferability of lotic fish SDMs when evaluated across all 25 species in our study. However, there was limited, though not statistically significant, evidence of higher transferability for invertivores than omnivores and invertivores/piscivores when we limited analysis to feeding strategies with at least three species. This finding was consistent with Dobrowski et al. (2011) and Huang and Frimpong (2016), who suggested that transferability is likely higher for species with low trait plasticity or highly specialized traits. Our results were similar to Huang et al. (2016) in that family was not an important predictor of transferability in either study, but differed in that Huang et al. (2016) identified an effect of temperature preference on transferability. The lack of strong, consistent effects of species characteristics on transferability among studies may indicate that transferability is species- and context-specific rather than predictable based on species characteristics, but the effects of traits on transferability may warrant further investigation given the potential

differences in transferability among feeding guilds (this study) and temperature preferences (Huang et al. 2016).

Comparisons of SDMs among basins suggested that MRB SDMs were more likely to transfer when they contained variables of high importance (i.e., delta deviance) in CRB SDMs and when species-environment relationships were consistent among basins, but high variable overlap and correlated variable importance among SDMs were unnecessary for effective transferability. First, we found that MRB SDMs that transferred effectively typically included variables with higher variable importance in CRB SDMs than SDMs that did not transfer. This result was consistent with Leftwich et al. (1997), who hypothesized that different limiting factors between streams resulted in low transferability of habitat relationships for Tangerine Darters *Percina aurantiaca*. Second, of the eight species whose most important variable in SDMs was mean annual air temperature in both basins, we found that the effect temperature was generally more consistent between basins for the five SDMs that transferred than for the three SDMs that did not transfer. Similar to our results, Huang and Frimpong (2016) found that transferability relied on consistent species-environment relationships between regions. Contrary to our expectations, variable overlap between SDMs (i.e., percent of variables from CRB SDM that were included in MRB SDM) was generally lower for SDMs that transferred effectively than for SDMs that did not transfer. Finally, correlated variable importance among SDMs could be a useful predictor of SDM transferability but is not essential for SDM transferability because only 2 of the 15 species whose SDMs transferred between basins exhibited correlated variable importance.

The complexity and directness of fish-environment relationships likely affect transferability of lotic fish SDMs. First, variables with direct relationships to organisms are likely more transferable than variables with indirect effects (Murray et al. 2011; Wenger and Olden 2012; Gies et al. 2015; Huang and Frimpong 2016). For example, Huang and Frimpong (2016) hypothesized that temperature, altitude, and hydrological conditions were frequently identified as important predictors due to their direct effects on survival, growth, and reproduction, but variables representing anthropogenic activities were generally less transferable. Therefore, although we found that temperature, base-flow index, precipitation, and mean annual streamflow were often important variables in SDMs in both basins, omitting anthropogenic predictor variables from SDMs may have improved transferability. Second, simple modeling approaches and species-environment relationships are likely more transferable than complex approaches and relationships (Wenger and Olden 2012; Iturbide et al. 2018). Therefore, although MARS models may have optimized model fit in the MRB, their ability to estimate complex relationships may have reduced their predictive performance in the CRB. Finally, although we identified more-complex species-temperature relationships in the MRB than CRB for Red Shiner and Yellow Bullhead, these models transferred reasonably well. This was likely due to a general positive relationship between species occurrence and temperature in both basins for both species.

Transferability of SDMs is most likely for species that exhibit high niche conservatism and have narrow niche breadth. A fundamental assumption to transferability is that a species' niche-related traits do not change over time or spatial scales relevant to the study (i.e., niche conservatism; Wiens and Graham 2005; Olden et

al. 2010). This assumption is consistent with our finding that models generally transferred across basins when the variables driving distributions and their effects were consistent between basins. Likewise, species exhibiting wide niche breadth (i.e., ability to use a wide range of habitats or resources; Slatyer et al. 2013) are likely to have lower SDM transferability than highly specialized species because they can use different resources in different regions without fundamental changes to their ecological traits. This hypothesis was supported by our limited evidence of lower SDM transferability for generalist feeding strategies than for species with more specialized feeding strategies and by Dobrowski et al. (2011), who found lower model transferability for plant species with specialized adaptations to fire.

Our estimates of lotic fish SDM transferability were likely biased by habitat connectivity, the extent of species introductions, and the equilibrium status of the species with the environment. Our model predictions likely over-estimated realized distributions in the CRB, and subsequently underestimated transferability, because we assumed that species had access to the entire CRB through natural movements or species introductions. However, lack of connectivity (Filipe et al. 2013) and lack of introductions would result in species absences in suitable stream reaches because the species did not have an opportunity to colonize those reaches. Furthermore, transferability would be biased if the species was not in equilibrium with its environment in either region (Elith and Leathwick 2009; Huang and Frimpong 2016). For example, our transferability estimates would be biased low if our models correctly identified reaches as unsuitable for a species where it was caught, but the species was recently introduced and did not successfully establish a self-sustaining population.

In summary, we found that lotic fish SDMs may be transferred in space and that transferability may differ among feeding strategies but not among the other species characteristics we evaluated. To our knowledge, this was the first study to evaluate the effects of species traits on spatial SDM transferability of lotic fishes, although Huang et al. (2016) evaluated the effects of temperature preference on temporal SDM transferability. Our findings highlight the need to use caution when transferring SDMs spatially, and the need to evaluate transferability when using SDM predictions to inform non-native species management. Although it may not be possible to test SDM transferability to an area where a species has not been introduced, evaluating transferability of SDMs based on a subset of the species' range to its remaining range may provide valuable insight into the validity of using SDM predictions to address non-native species challenges.

Our study reinforces that a tradeoff exists between SDM predictive ability where the model was developed and transferability to new areas (Elith and Leathwick 2009; Iturbide et al. 2018). Multiple studies indicated that simple modeling approaches had higher transferability than complex modeling approaches (Wenger and Olden 2012; Huang and Frimpong 2016; Iturbide et al. 2018). Similarly, we found that complex MARS SDMs had high predictive ability in the MRB, but had limited transferability to the CRB for numerous species. Therefore, researchers may maximize transferability by using simple modeling approaches. Second, SDMs developed with predictor variables that have direct ecological links to species ecology likely have higher transferability than SDMs that include variables with complex or indirect ecological effects (Murray et al. 2011; Wenger and Olden 2012; Gies et al. 2015; Huang and Frimpong 2016), but

omitting potentially ecologically important variables from SDMs may limit SDM predictive ability if these variables are important drivers of species distributions where the models were developed. In conclusion, using simple modeling approaches and variables with direct ecological linkages may increase transferability, but may also decrease performance where SDMs were developed.

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Tables

Table 3.1. Landscape-scale environmental variables used as predictor variables in multivariate adaptive regression spline species distribution models in the Missouri River (MRB) and Colorado River (CRB) basins. Variables without a code were excluded from models because they were highly correlated with other variables.

Variable	Scale	Source	Variable Code	CRB			MRB		
				Min	Max	Median	Min	Max	Median
Strahler stream order	Segment	USEPA 2005	SO	1	4	2	1	4	3
Average base-flow index for each catchment (%)	Segment	Wieczorek and LaMotte 2010a	BFI	2.0	78.9	59.3	8.0	85.0	45.0
Mean annual flow (cfs) at bottom of flowline as computed by Unit Runoff Method	Segment	USEPA and USGS 2005	Flow	0.0	655.3	4.0	0.0	409.3	3.2
Mean annual velocity (fps) at bottom of flowline as computed by Unit Runoff Method	Segment	USEPA and USGS 2005	Velo	0.1	2.9	1.2	0.4	2.1	1.0
Mean slope (%)	Local catchment	Wieczorek and LaMotte 2010b	Slope	0.4	118.8	23.6	0.0	69.0	7.1
Mean elevation (m)	Local catchment	Wieczorek and LaMotte 2010b		140.7	3821.6	2335.6	148.3	2957.0	794.6
Number of dams in catchment	Local catchment	Esselman et al. 2011a	L_Dam	0.0	3.0	0.0	0.0	17.0	0.0
Percent of catchment defined as cultivated crops	Local catchment	Esselman et al. 2011a		0.0	78.5	0.0	0.0	100.0	1.2
Percent of catchment defined as urban	Local catchment	Esselman et al. 2011a		0.0	99.9	0.0	0.0	100.0	2.1
Mean population density within catchment (#/km ²)	Local catchment	Esselman et al. 2011a		0.0	1455.2	0.5	0.0	820.4	0.8

Variable	Scale	Source	Variable Code	CRB			MRB		
				Min	Max	Median	Min	Max	Median
The 30-year (1981-2010) average annual normal precipitation (mm) within the total upstream watershed	Network watershed	USEPA 2015	Precip	123.6	1556.3	682.0	156.5	1688.3	756.5
The 30-year (1981-2010) average annual normal minimum air temperature (°C) within the total upstream watershed	Network watershed	USEPA 2015		-8.0	15.8	-2.6	-7.2	7.8	0.2
The 30-year (1981-2010) average annual normal maximum air temperature (°C) within the total upstream watershed	Network watershed	USEPA 2015		4.7	30.7	11.5	3.8	19.8	14.6
The 30-year (1981-2010) average annual normal mean air temperature (°C) within the total upstream watershed	Network watershed	USEPA 2015	Temp	-1.5	23.2	4.5	-1.7	13.8	7.5
Percent of watershed defined as non-carbonate surficial lithology	Network watershed	Cress et al. 2010	Lit3	0.0	100.0	41.1	0.0	100.0	30.5
Percent of watershed defined as silicic surficial lithology	Network watershed	Cress et al. 2010	Lit5	0.0	100.0	15.6	0.0	100.0	0.0
Percent of watershed defined as alluvium and fine-textured coastal zone sediment surficial lithology	Network watershed	Cress et al. 2010	Lit19	0.0	100.0	0.0	0.0	100.0	0.0
Number of dams in watershed	Network watershed	Esselman et al. 2011a	N_Dam	0.0	86.0	0.0	0.0	1285.0	0.0
Percent of watershed defined as cultivated crops	Network watershed	Esselman et al. 2011a	N_Crop	0.0	75.8	0.0	0.0	97.3	2.7
Percent of watershed defined as urban	Network watershed	Esselman et al. 2011a	N_Urban	0.0	99.9	0.0	0.0	92.6	1.8
Mean population density within watershed (#/km ²)	Network watershed	Esselman et al. 2011a	N_Pop	0.0	1325.6	0.5	0.0	893.5	0.6

Table 3.2. Species characteristics, performance of multivariate adaptive regression spline species distribution models developed for the Missouri (MRB) and Colorado River (CRB) basins quantified as the area under the receiver-operating curve (AUC), model transferability from the MRB to the entire CRB (MRB→CRB) and ecological drainage units (EDU) that the species occurred [MRB→CRB (EDU)], and the difference in AUC between transferability MRB→CRB (EDU) and MRB→CRB [Δ (EDU)]. I=non-native; N=native for nativity. G_NS= guarder, nest spawner; NG_OS= non-guarder, open substratum spawner, B_E= external bearer, NG_BH= non-guarder, brood hider for reproductive guild.

	Species Code	Common Name	Scientific Name	Family	Nativity		Temperature Preference	Substrate Preference	Reproductive Guild	Trophic Guild	AUC				
											MRB	CRB	MRB→CRB	MRB→CRB (EDU)	Δ (EDU)
					CRB	MRB									
∞	AMME	Black Bullhead	Ameiurus melas	Ictaluridae	I	N	Warm	Silt/ mud	G_NS	Invertivore/piscivore	0.841	0.921	0.755	0.734	-0.021
	AMNA	Yellow Bullhead	Ameiurus natalis	Ictaluridae	I	N	Warm	Rubble	G_NS	Invertivore/piscivore	0.906	0.960	0.883	0.673	-0.210
	CACA	Longnose Sucker	Catostomus catostomus	Catostomidae	I	N	Cool	Rubble	NG_OS	Omnivore	0.935	0.938	0.697	0.651	-0.046
	CACO	White Sucker	Catostomus commersonii	Catostomidae	I	N	Cool	General	NG_OS	Omnivore	0.824	0.898	0.746	0.756	0.010
	CAPT	Mountain Sucker	Catostomus platyrhynchus	Catostomidae	N	N	Cool	Rubble	NG_OS	Herbivore/detritivore	0.965	0.903	0.606	0.668	0.062
	COBA	Mottled Sculpin	Cottus bairdii	Cottidae	N	N	Cold	Rubble	NG_BH	Invertivore	0.912	0.884	0.742	0.611	-0.131
	COPL	Lake Chub	Couesius plumbeus	Cyprinidae	I	N	Cool	Sand	NG_OS	Invertivore	0.952	0.990	0.865	0.762	-0.103
	CUIN	Brook Stickleback	Culaea inconstans	Gasterosteidae	I	N	Cool	Silt/ mud	G_NS	Invertivore	0.966	0.971	0.747	0.694	-0.053
	CYCA	Common Carp	Cyprinus carpio	Cyprinidae	I	I	Warm	Silt/ mud	NG_OS	Omnivore	0.851	0.836	0.713	0.732	0.019
	CYLU	Red Shiner	Cyprinella lutrensis	Cyprinidae	I	N	Warm	General	NG_OS	Invertivore	0.958	0.905	0.833	0.824	-0.009
	ETNI	Johnny Darter	Etheostoma nigrum	Percidae	I	N	Cool	Sand	G_NS	Invertivore	0.932	1.000	0.842	0.885	0.043
	GAAF	Western Mosquitofish	Gambusia affinis	Poeciliidae	I	I	Warm	Silt/ mud	B_E	Invertivore	0.927	0.946	0.926	0.896	-0.030
	ICPU	Channel Catfish	Ictalurus punctatus	Ictaluridae	I	N	Warm	Silt/ mud	G_NS	Invertivore/piscivore	0.914	0.904	0.590	0.550	-0.040

Species Code	Common Name	Scientific Name	Family	Nativity		Temperature Preference	Substrate Preference	Reproductive Guild	Trophic Guild	AUC				
				CRB	MRB					MRB	CRB	MRB → CRB	MRB → CRB (EDU)	Δ (EDU)
LECY	Green Sunfish	Lepomis cyanellus	Centrarchidae	I	N	Warm	Silt/ mud	G_NS	Invertivore/ piscivore	0.926	0.910	0.824	0.772	-0.052
LEMA	Bluegill	Lepomis macrochirus	Centrarchidae	I	N	Warm	General	G_NS	Invertivore/ piscivore	0.949	0.880	0.681	0.656	-0.025
MISA	Largemouth Bass	Micropterus salmoides	Centrarchidae	I	N	Warm	Silt/ mud	G_NS	Piscivore	0.926	0.961	0.777	0.749	-0.028
NOCR	Golden Shiner	Notemigonus crysoleucas	Cyprinidae	I	N	Warm	Silt/ mud	NG_OS	Omnivore	0.889	0.729	0.666	0.594	-0.072
NOST	Sand Shiner	Notropis stramineus	Cyprinidae	I	N	Warm	Rubble	NG_OS	Omnivore	0.914	0.942	0.680	0.818	0.138
ONCL	Cutthroat Trout	Oncorhynchus clarkii	Salmonidae	N	N	Cold	Rubble	NG_BH	Invertivore/ piscivore	0.954	0.878	0.811	0.765	-0.046
ONMY	Rainbow Trout	Oncorhynchus mykiss	Salmonidae	I	I	Cold	Rubble	NG_BH	Invertivore/ piscivore	0.893	0.816	0.697	0.695	0.002
PIPR	Fathead Minnow	Pimephales promelas	Cyprinidae	I	N	Warm	Silt/ mud	G_NS	Omnivore	0.907	0.845	0.689	0.689	0.000
RHCA	Longnose Dace	Rhinichthys cataractae	Cyprinidae	I	N	Cool	Rubble	NG_OS	Invertivore	0.943	0.905	0.741	0.704	-0.037
SAFO	Brook Trout	Salvelinus fontinalis	Salmonidae	I	I	Cold	Rubble	NG_BH	Invertivore/ piscivore	0.946	0.872	0.690	0.684	-0.006
SATR	Brown Trout	Salmo trutta	Salmonidae	I	I	Cold	Rubble	NG_BH	Invertivore/ piscivore	0.909	0.861	0.718	0.712	-0.006
SEAT	Creek Chub	Semotilus atromaculatus	Cyprinidae	I	N	Cool	Rubble	G_NS	Invertivore/ piscivore	0.929	0.925	0.667	0.757	0.090

Table 3.3. Total number of species, number and percent of species whose multivariate adaptive regression spline species distribution models transferred from the Missouri River Basin to the Colorado River Basin, and average and standard deviation (SD) of area under the receiver-operating curve (AUC) values by species characteristic.

Category	Group	Species			AUC	
		Total	Transferred (n)	Transferred (%)	Average	SD
Native	Non-native	22	13	59	0.75	0.08
	Native	3	2	67	0.72	0.10
Temperature	Cold	5	3	60	0.73	0.05
	Cool	8	5	63	0.74	0.09
	Warm	12	7	58	0.75	0.10
Substrate	General	3	2	67	0.75	0.08
	Rubble	11	5	45	0.72	0.07
	Sand	2	2	100	0.85	0.02
	Silt/mud	9	6	67	0.74	0.10
Reproductive guild	External bearer	1	1	100	0.93	-
	Guarder, nest spawner	10	6	60	0.75	0.09
	Non-guarder, brood hider	5	3	60	0.73	0.05
	Non-guarder, open substratum spawner	9	5	56	0.73	0.08
Trophic feeding guild	Herbivore/detritivore	1	0	0	0.61	-
	Invertivore/piscivore	10	5	50	0.73	0.09
	Invertivore	7	7	100	0.81	0.07
	Omnivore	6	2	33	0.70	0.03
	Piscivore	1	1	100	0.78	-
Family	Catostomidae	3	1	33	0.68	0.07
	Centrarchidae	3	2	67	0.76	0.07
	Cottidae	1	1	100	0.74	-
	Cyprinidae	8	4	50	0.73	0.08
	Gasterosteidae	1	1	100	0.75	-
	Ictaluridae	3	2	67	0.74	0.15
	Percidae	1	1	100	0.84	-
	Poeciliidae	1	1	100	0.93	-
	Salmonidae	4	2	50	0.73	0.06

Table 3.4. Variable importance (delta deviance) of multivariate adaptive regression spline species distribution models (SDMs) developed in the Missouri (MRB) and Colorado (CRB) River basins by species and basin. Variable descriptions are available in Table 3.1 and species codes are in Table 3.2. Darker shading indicates higher values for each column. An asterisk (*) indicates species whose SDMs transferred from the CRB to MRB. Column subheadings MRB and CRB indicate the basin that SDMs were developed.

Variable Code	Species-Basin																	
	AMME*		AMNA*		CACA		CACO*		CAPT		COBA*		COPL*		CUIN*		CYCA*	
	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB
SO	0	37.1	73.5	0	0	0	0	0	39.8	0	40.9	0	0	0	34.7	30	45.3	51.6
L_Dam	0	0	0	0	0	0	0	0	0	0	22.5	0	0	0	0	0	0	22.4
N_Crop	100	31.9	0	0	0	0	50.6	24.2	26.3	37.9	0	100	0	27.5	88.4	26.3	48.7	57.1
N_Pop	0	0	77.7	21	0	0	0	0	62	0	0	0	80.4	0	0	0	81	0
N_Dam	10.2	0	0	26.1	14.2	0	23.8	50.9	0	42	0	0	0	14.1	64.3	0	0	100
N_Urban	0	34.1	0	0	0	37.4	0	0	0	0	0	59.8	21.4	31.1	0	63.1	0	33.1
BFI	13.2	100	48.2	32.6	23.9	60.4	17.1	56.6	0	95.4	32.7	76.2	48.8	54.2	82.4	5.1	73.9	39.1
Flow	0	49.4	62.8	38.8	100	17.3	100	60.9	82.5	100	100	28.3	77.8	41.3	0	12.2	0	41.2
Velo	0	18.3	0	11.6	48.3	100	50.7	7.1	43.1	0	27.9	0	72.9	5.2	38.8	0	20.1	0
Precip	0	26.2	72.7	0	17.7	82.3	34.9	33.2	41	0	24.9	79.2	54.2	100	18	100	100	30.3
Temp	16.3	69.2	100	100	36.6	0	61.9	100	41	92.4	70	63.3	95.4	28.7	0	58.9	71.8	75.7
Slope	36.3	41.7	0	0	26.6	47.2	74.8	37	69.6	0	18.4	21.7	100	11.9	45.1	0	56	0
Lit19	32.3	0	38.2	0	0	0	29.4	0	0	0	0	0	0	0	0	8.9	0	36.3
Lit3	23.8	0	35.1	0	0	33.1	0	0	34.5	33.5	36.9	42.2	0	0	100	15.2	0	0
Lit5	0	0	58	0	41	26.7	0	0	100	0	0	0	37.6	0	0	0	0	0

Table 3.4 (continued).

Variable	Species-Basin															
	CYLU*		ETNI*		GAAF*		ICPU		LECY*		LEMA		MISA*		NOCR	
	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB
SO	15.6	0	0	0	0	14.9	0	26.3	0	0	0	0	0	0	0	0
L_Dam	0	0	0	0	0	0	0	0	0	0	0	0	0	17.2	0	36.7
N_Crop	0	44	100	60.7	62.7	28.8	0	0	60.2	0	41.3	17.1	100	24.8	0	62.7
N_Pop	0	0	0	0	0	17.7	0	0	69.9	0	87.7	17.1	62.7	0	71	0
N_Dam	0	0	0	0	0	31	0	100	0	0	0	14.6	0	19.7	38	0
N_Urban	0	12.3	0	53.2	0	12.4	0	19.2	26.1	0	0	8.2	0	23.9	83.8	49.5
BFI	93.9	33.3	0	100	77.6	0	100	33.1	64.2	28.8	35.3	31.4	0	39	30.3	35.7
Flow	64	36.8	63.7	41.4	0	23.1	0	44.4	48.4	9.5	17.7	14.3	27.1	32.5	0	16.4
Velo	0	18.5	0	12.2	0	20.4	67.6	39.4	0	7.5	0	9.5	42.9	14.2	0	0
Precip	55.9	66.6	0	72.2	27	0	31.4	57.6	0	24.3	0	25.9	0	29.3	0	53.4
Temp	100	100	0	48.2	100	100	0	64.4	100	100	100	100	72.4	100	100	100
Slope	0	0	42.3	0	0	32.2	99.1	21.3	0	0	0	0	34.7	0	0	20
Lit19	0	14.2	0	0	21.4	45.1	39.6	15.5	0	0	0	0	38.3	0	0	0
Lit3	0	0	0	34.6	0	0	0	0	0	0	25.5	11.9	23.4	0	0	0
Lit5	0	0	0	0	0	0	0	0	30.4	0	0	0	9	0	0	0

Table 3.4 (continued).

Variable	Species-Basin															
	NOST		ONCL*		ONMY		PIPR		RHCA*		SAFO		SATR*		SEAT	
	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB
SO	0	32.8	30.3	6.6	43.9	37.5	49.6	0	0	0	10.6	0	32.2	16.3	75	0
L_Dam	0	0	10.5	0	0	0	18.3	0	0	0	0	0	7.6	0	0	0
N_Crop	100	17.9	0	0	32.9	0	87.4	30.3	36.5	42.3	0	0	0	47.9	34.4	9.4
N_Pop	0	25.6	0	0	22	0	0	0	0	0	15.5	0	0	0	0	13.5
N_Dam	0	29.8	0	0	0	0	100	13.1	73.3	25.3	18.3	0	0	0	0	29
N_Urban	0	0	0	0	0	0	0	21.2	0	38.3	0	15	18.7	40.5	0	20.3
BFI	0	40.2	18.6	28.9	14.9	100	75.3	82.5	0	54.9	13	34.2	49.1	73.8	63.5	33.6
Flow	0	40.2	63.1	10	100	26.8	25.5	0	100	16	34.3	0	100	0	0	7.6
Velo	0	8.7	27.1	8.7	0	72.4	49.6	6.8	58.9	66.7	0	17.5	0	100	12.1	10.3
Precip	0	55.5	13.1	19.4	74.8	41.9	0	18.5	0	31.7	13.9	38.3	21.4	44.9	40.5	45.8
Temp	0	100	100	100	52.5	52.2	28.7	100	19.6	100	100	100	38.1	54.4	75.9	100
Slope	26.5	17.9	35.2	32.1	0	0	50.1	15.4	0	22.6	0	24.8	15.7	53.3	85.8	23.3
Lit19	22.9	12	0	0	27.3	14.7	0	0	39.4	0	20.3	8.1	0	0	55.1	0
Lit3	67.2	0	49.4	24	54.5	0	0	13.1	0	13.5	27.5	0	52.6	28.9	100	12.2
Lit5	0	0	24.1	12.2	54.5	23.8	39.3	13.1	31	0	11.8	19.7	44	32	17.1	0

Figures

Figure 3.1. Number of multivariate adaptive regression spline species distribution models (SDMs) that a variable occurred (top) and mean importance (delta deviance) of variables that were included in SDMs (i.e., zeros excluded; bottom) for the Colorado (CRB) and Missouri (MRB) River basins. See Table 3.1 for variable code descriptions. Line approximates 1:1.

Figure 3.2. Percent of variables from multivariate adaptive regression spline species distribution models (SDMs) developed from Colorado River basin (CRB) data that were in Missouri River basin (MRB) SDMs (i.e., variable overlap) and mean variable importance (delta deviance) of variables in CRB SDMs for variables that occurred in SDMs for both basins. Each point represents one species and is labeled by MRB SDM transferability: low = $AUC < 0.7$, high = $AUC \geq 0.7$.

Figure 3.3. Variable importance (delta deviance) of multivariate adaptive regression spline species distribution models (SDMs) developed for the Colorado (CRB) and Missouri (MRB) River basins for species whose SDMs transferred from the MRB to CRB.

Figure 3.4. Variable importance of multivariate adaptive regression spline species distribution models (SDMs) developed for the Colorado (CRB) and Missouri (MRB) River basins for species whose SDMs did not transfer from the MRB to CRB.

Figure 3.5. Predicted effect of mean annual air temperature on probability of occurrence for eight species whose most important variable in Colorado River (CRB) and Missouri River (MRB) basin multivariate adaptive regression spline species distribution models (SDMs) was mean annual temperature. Values represent the probability of occurrence at median values of all other environmental variables. Grey area represents temperatures available in CRB that are outside the temperature range available in the MRB. An asterisk (*) indicates species whose SDMs transferred from the MRB to the CRB.

Appendices

Appendix 3.1. Mean variable importance of multivariate adaptive regression spline species distribution models (SDMs) developed in the Colorado (CRB) and Missouri (MRB) River basins by family and basin. Variable code descriptions are available in Table 3.1. Darker shading indicates higher values for each column. Column subheadings MRB and CRB indicate the basin that SDMs were developed.

Variable Code	Catostomidae		Centrarchidae		Cottidae		Cyprinidae		Gasterosteidae		Ictaluridae		Percidae		Poeciliidae		Salmonidae	
	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB
BFI	13.7	70.8	33.2	33.1	32.7	76.2	48.2	46.7	82.4	5.1	53.8	55.2	0.0	100.0	77.6	0.0	23.9	59.2
Flow	94.2	59.4	31.1	18.8	100.0	28.3	33.4	24.9	0.0	12.2	20.9	44.2	63.7	41.4	0.0	23.1	74.4	9.2
L_Dam	0.0	0.0	0.0	5.7	22.5	0.0	2.3	7.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.5	0.0
Lit19	9.8	0.0	12.8	0.0	0.0	0.0	14.7	7.8	0.0	8.9	36.7	5.2	0.0	0.0	21.4	45.1	11.9	5.7
Lit3	11.5	22.2	16.3	4.0	36.9	42.2	20.9	4.9	100.0	15.2	19.6	0.0	0.0	34.6	0.0	0.0	46.0	13.2
Lit5	47.0	8.9	13.1	0.0	0.0	0.0	15.6	1.6	0.0	0.0	19.3	0.0	0.0	0.0	0.0	0.0	33.6	21.9
N_Crop	25.6	20.7	67.2	14.0	0.0	100.0	38.4	36.4	88.4	26.3	33.3	10.6	100.0	60.7	62.7	28.8	8.2	12.0
N_Dam	12.7	31.0	0.0	11.4	0.0	0.0	26.4	26.4	64.3	0.0	3.4	42.0	0.0	0.0	0.0	31.0	4.6	0.0
N_Pop	20.7	0.0	73.4	5.7	0.0	0.0	29.1	4.9	0.0	0.0	25.9	7.0	0.0	0.0	0.0	17.7	9.4	0.0
N_Urban	0.0	12.5	8.7	10.7	0.0	59.8	13.2	25.7	0.0	63.1	0.0	17.8	0.0	53.2	0.0	12.4	4.7	13.9
Precip	31.2	38.5	0.0	26.5	24.9	79.2	31.3	50.2	18.0	100.0	34.7	27.9	0.0	72.2	27.0	0.0	30.8	36.1
Slope	57.0	28.1	11.6	0.0	18.4	21.7	39.8	13.9	45.1	0.0	45.1	21.0	42.3	0.0	0.0	32.2	12.7	27.6
SO	13.3	0.0	0.0	0.0	40.9	0.0	23.2	10.6	34.7	30.0	24.5	21.1	0.0	0.0	0.0	14.9	29.3	15.1
Temp	46.5	64.1	90.8	100.0	70.0	63.3	61.4	88.1	0.0	58.9	38.8	77.9	0.0	48.2	100.0	100.0	72.7	76.7
Velo	47.4	35.7	14.3	10.4	27.9	0.0	26.7	14.5	38.8	0.0	22.5	23.1	0.0	12.2	0.0	20.4	6.8	49.7

Appendix 3.2. Mean variable importance of multivariate adaptive regression spline species distribution models (SDMs) developed in the Colorado (CRB) and Missouri (MRB) River basins by species nativity and basin. Variable code descriptions are available in Table 3.1. Darker shading indicates higher values for each column. Column subheadings MRB and CRB indicate the basin that SDMs were developed.

Variable Code	CRB Nativity				MRB Nativity			
	Non-native		Native		Non-native		Native	
	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB
BFI	42.0	48.6	17.1	66.8	45.7	49.4	37.4	51.1
Flow	41.9	25.9	81.9	46.1	46.9	18.2	46.6	30.9
L_Dam	1.2	3.5	11.0	0.0	1.5	4.5	2.6	2.7
Lit19	16.6	7.0	0.0	0.0	13.8	20.8	14.8	2.5
Lit3	23.2	7.4	40.3	33.2	26.9	5.8	24.8	11.7
Lit5	17.0	5.2	41.4	4.1	22.1	15.1	19.4	2.6
N_Crop	42.9	25.1	8.8	46.0	28.9	26.8	41.3	27.9
N_Dam	15.6	20.6	0.0	14.0	3.7	26.2	16.2	18.2
N_Pop	25.8	4.3	20.7	0.0	23.7	3.5	25.6	3.9
N_Urban	6.8	23.3	0.0	19.9	3.7	20.2	6.6	23.6
Precip	25.6	44.5	26.3	32.9	47.4	31.1	20.2	46.1
Slope	31.5	16.8	41.1	17.9	14.3	22.1	37.2	15.6
SO	17.3	11.2	37.0	2.2	26.4	24.1	18.0	6.6
Temp	57.7	79.6	70.3	85.2	72.5	76.5	55.9	81.3
Velo	21.0	24.8	32.7	2.9	4.0	42.1	27.0	17.2

Appendix 3.3. Mean variable importance of multivariate adaptive regression spline species distribution models (SDMs) developed in the Colorado (CRB) and Missouri (MRB) River basins by feeding guild and basin. Variable code descriptions are available in Table 3.1. Darker shading indicates higher values for each column. Column subheadings MRB and CRB indicate the basin that SDMs were developed.

Variable Code	Herbivore/ detritivore		Invertivore/ piscivore		Invertivore		Omnivore		Piscivore	
	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB
BFI	0.0	95.4	42.0	49.6	47.9	46.2	36.8	52.4	0.0	39.0
Flow	82.5	100.0	42.6	20.1	57.9	28.4	37.6	29.3	27.1	32.5
L_Dam	0.0	0.0	1.8	0.0	3.2	0.0	3.1	9.9	0.0	17.2
Lit19	0.0	0.0	21.3	3.8	8.7	9.7	8.7	8.1	38.3	0.0
Lit3	34.5	33.5	36.8	7.7	19.6	15.1	11.2	7.7	23.4	0.0
Lit5	100.0	0.0	24.0	8.8	9.8	0.0	13.4	6.6	9.0	0.0
N_Crop	26.3	37.9	26.9	10.6	41.1	47.1	47.8	32.0	100.0	24.8
N_Dam	0.0	42.0	2.9	17.0	19.7	10.1	29.3	32.3	0.0	19.7
N_Pop	62.0	0.0	27.3	5.2	11.5	2.5	25.3	4.3	62.7	0.0
N_Urban	0.0	0.0	4.5	13.7	3.1	38.6	14.0	23.5	0.0	23.9
Precip	41.0	0.0	26.8	32.4	25.7	64.2	25.4	45.5	0.0	29.3
Slope	69.6	0.0	27.2	19.7	29.4	12.6	39.0	22.9	34.7	0.0
SO	39.8	0.0	26.6	12.4	13.0	6.4	15.8	14.1	0.0	0.0
Temp	41.0	92.4	68.3	84.0	55.0	71.3	49.8	79.3	72.4	100.0
Velo	43.1	0.0	10.7	29.5	28.4	17.6	28.1	20.4	42.9	14.2

Appendix 3.4. Mean variable importance of multivariate adaptive regression spline species distribution models (SDMs) developed in the Colorado (CRB) and Missouri (MRB) River basins by substrate preference and basin. Variable code descriptions are available in Table 3.1. Darker shading indicates higher values for each column. Column subheadings MRB and CRB indicate the basin that SDMs were developed.

Variable Code	General		Rubble		Sand		Silt/mud	
	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB
BFI	48.8	40.4	24.0	57.3	24.4	77.1	57.4	40.4
Flow	60.6	37.3	67.5	25.9	70.8	41.4	11.2	25.4
L_Dam	0.0	0.0	3.7	0.0	0.0	0.0	2.0	8.5
Lit19	9.8	4.7	18.5	3.2	0.0	0.0	14.6	11.8
Lit3	8.5	4.0	41.6	17.0	0.0	17.3	16.4	3.1
Lit5	0.0	0.0	34.7	10.4	18.8	0.0	8.7	1.5
N_Crop	30.6	28.4	20.9	23.2	50.0	44.1	60.8	29.1
N_Dam	7.9	21.8	9.6	13.8	0.0	7.1	23.6	29.3
N_Pop	29.2	5.7	16.1	5.5	40.2	0.0	31.6	2.0
N_Urban	0.0	6.8	1.7	19.2	10.7	42.2	12.2	28.5
Precip	30.3	41.9	29.1	39.9	27.1	86.1	19.6	37.7
Slope	24.9	12.3	25.3	22.1	71.2	6.0	35.7	14.5
SO	5.2	0.0	31.5	8.5	0.0	0.0	14.4	17.8
Temp	87.3	100.0	57.6	78.4	47.7	38.5	54.4	85.4
Velo	16.9	11.7	19.8	36.0	36.5	8.7	24.3	11.8

Appendix 3.5. Mean variable importance of multivariate adaptive regression spline species distribution models (SDMs) developed in the Colorado (CRB) and Missouri (MRB) River basins by temperature preference and basin. Variable code descriptions are available in Table 3.1. Darker shading indicates higher values for each column. Column subheadings MRB and CRB indicate the basin that SDMs were developed.

Variable Code	Cold		Cool		Warm	
	CRB	MRB	CRB	MRB	CRB	MRB
BFI	25.7	62.6	29.5	57.5	51.0	41.3
Flow	79.5	13.0	65.5	37.1	20.5	28.9
L_Dam	8.1	0.0	0.0	0.0	1.5	6.4
Lit19	9.5	4.6	15.5	1.1	16.1	10.3
Lit3	44.2	19.0	29.3	17.8	14.6	2.1
Lit5	26.9	17.5	28.3	3.3	11.4	1.1
N_Crop	6.6	29.6	42.0	28.5	50.0	26.2
N_Dam	3.7	0.0	22.0	20.2	12.4	27.9
N_Pop	7.5	0.0	17.8	1.7	37.5	6.8
N_Urban	3.7	23.1	2.7	30.4	9.2	17.8
Precip	29.6	44.7	25.8	58.2	23.9	32.3
Slope	13.9	26.4	55.5	17.8	25.2	12.4
SO	31.6	12.1	18.7	3.8	15.3	13.6
Temp	72.1	74.0	41.3	66.0	65.8	92.4
Velo	11.0	39.7	40.6	25.2	15.0	12.9

Appendix 3.6. Mean variable importance of multivariate adaptive regression spline species distribution models (SDMs) developed in the Colorado (CRB) and Missouri (MRB) River basins by reproductive guild and basin. Variable code descriptions are available in Table 3.1. Darker shading indicates higher values for each column. Column subheadings MRB and CRB indicate the basin that SDMs were developed.

Variable Code	External bearer		Guarder, nest-spawner		Non-guarder, brood hider		Non-guarder, open substrate	
	CRB	MRB	CRB	MRB	CRB	MRB	CRB	MRB
BFI	77.6	0.0	48.2	48.6	25.7	62.6	32.0	52.2
Flow	0.0	23.1	24.5	25.0	79.5	13.0	58.3	41.1
L_Dam	0.0	0.0	1.8	1.7	8.1	0.0	0.0	6.6
Lit19	21.4	45.1	20.4	2.4	9.5	4.6	10.2	6.9
Lit3	0.0	0.0	30.8	8.7	44.2	19.0	11.3	8.9
Lit5	0.0	0.0	15.4	1.3	26.9	17.5	23.3	3.0
N_Crop	62.7	28.8	61.2	20.1	6.6	29.6	29.1	34.8
N_Dam	0.0	31.0	17.5	20.3	3.7	0.0	16.6	29.1
N_Pop	0.0	17.7	29.8	5.2	7.5	0.0	32.7	2.8
N_Urban	0.0	12.4	2.6	24.3	3.7	23.1	11.7	22.4
Precip	27.0	0.0	16.3	40.0	29.6	44.7	33.7	50.3
Slope	0.0	32.2	39.3	10.2	13.9	26.4	39.3	17.4
SO	0.0	14.9	23.3	9.3	31.6	12.1	11.2	9.4
Temp	100.0	100.0	49.3	84.1	72.1	74.0	58.5	77.4
Velo	0.0	20.4	21.1	13.0	11.0	39.7	32.7	22.9

CHAPTER 4- FAMILY-LEVEL EVALUATION OF THE DRIVERS OF NON-NATIVE LOTIC FISH ESTABLISHMENT

Abstract

Non-native species are a primary factor leading to the decline of native fish species, and prevention of their establishment is often the most cost-effective control method for managing their effects on ecosystems. Human activity, biotic resistance, and biotic acceptance are three hypothesized drivers of non-native species establishment, but the drivers of non-native lotic fish species establishment are relatively unclear, potentially due to spatial and taxonomic scales of previous analyses. Therefore, we evaluated the Human Activity, Biotic Resistance, and Biotic Acceptance hypotheses for lotic fishes in the Missouri and Colorado River Basins at the “global” [i.e., Missouri and Colorado River basins (MRB and CRB, respectively) combined] and physiographic province spatial extents and family taxonomic level. Specifically, we evaluated the effects of human activity, biotic resistance and biotic acceptance metrics on the probability of non-native fish family occurrences with logistic regression for three families: Salmonidae, Catostomidae, and Cyprinidae. The drivers of non-native Salmonidae presence varied among spatial extents, but these hypotheses explained little variability in non-native Salmonidae presence (pseudo- $R^2 < 0.2$). Biotic Resistance and Biotic Acceptance hypotheses were the most-supported models of non-native Cyprinidae presence, but the variables that best explained non-native Cyprinidae presence differed between regions and only explained significant variability in one of five spatial extents (pseudo- $R^2 \geq 0.2$). Finally, the drivers of non-native Catostomidae presence varied among spatial extents, as

the Human Activity Hypothesis received the most support at the global extent and in the Intermontane Plateau physiographic division of the CRB, but the Biotic Acceptance Hypothesis was supported for the Interior Plains physiographic division of the MRB and Rocky Mountain System physiographic division (MRB and CRB). The hypothesized drivers generally explained little variability in non-native family occurrence, which may suggest that other factors (e.g., natural abiotic factors) are likely important drivers of non-native species at the spatial and taxonomic scales we considered. We suggest that considering non-native species invasions as a stepwise process within a hierarchical habitat filtering framework may provide valuable insight on the drivers of invasions, such as explaining variability in the drivers of invasions among spatial scales and species.

Introduction

Understanding the drivers of non-native fish establishment is critical to the conservation of native lotic fishes. Non-native species are a primary threat to native species and were implicated in the imperilment and extinction of numerous native lotic fishes (Miller et al. 1989; Tyus and Saunders 2000; Malmqvist and Rundle 2002). The threat posed by non-native fishes has likely increased recently in the USA because non-native fish species richness was predicted to increase from 69 in 1990 to 150 in 2025 (Malmqvist and Rundle 2002). However, identification of the factors that lead to non-native species establishment can reduce this threat by allowing areas with a high probability of establishment to be targeted for prevention efforts. The ability to identify and prioritize areas for prevention efforts is particularly valuable because prevention is often the most cost-effective approach for managing non-native species (Wittenberg and Cock 2001). Therefore, knowledge of the drivers of non-native species establishment is

critical to effective control of non-native species invasions and, subsequently, conservation of native fishes.

Three commonly evaluated hypotheses of the drivers of non-native species establishment are "Human Activity", "Biotic Acceptance", and "Biotic Resistance" (Olden et al. 2010). The Human Activity Hypothesis suggests that human activities promote non-native species by increasing propagule pressure (i.e., the number of species introductions or number of individuals introduced) and habitat alteration (Olden et al. 2010). The Biotic Acceptance Hypothesis suggests that environmental conditions that support a high diversity of native species will also support a high diversity of non-native species (Fridley et al. 2007). Finally, the Biotic Resistance Hypothesis predicts that ecosystems with high native species richness will be more resistant to non-native species (via competition and predation) than ecosystems with low native species richness, and therefore, will have fewer non-native species (Levine and D'Antonio 1999).

Currently, however, the drivers of non-native fish establishment are unclear, potentially due to different drivers among spatial scales or geographic regions. Dos Santos et al. (2018) indicated that an invasion paradox exists because there is support for two competing hypotheses (i.e., Biotic Resistance and Biotic Acceptance hypotheses) across taxa. These authors suggested that the paradox could be partially resolved by considering spatial scale because the Biotic Resistance Hypothesis is generally supported at small spatial scales (e.g., experimental scales) and the Biotic Acceptance Hypothesis tends to be supported at large spatial scales, though this pattern was primarily observed for terrestrial plants. Freshwater fish, however, may follow a different pattern because the Human Activity and Biotic Acceptance hypotheses have received support at multiple

spatial scales (Gido and Brown 1999; Meador et al. 2003; Marchetti et al. 2004; Light and Marchetti 2007; Leprieur et al. 2008; Blanchet et al. 2009; Hermoso et al. 2011; dos Santos et al. 2018). Furthermore, although negative relationships between native species richness and non-native species have been observed (e.g., Meador et al. 2003; Mitchell and Knouft 2009), it is difficult to determine whether these relationships represent Biotic Resistance, the negative effect of non-native species on native species, or differences in the number of non-native species introductions between areas (e.g. Gido et al. 2004). The lack of broad patterns in the drivers of non-native fish invasions may also be the result of different drivers (e.g., Blanchet et al. 2009) or colonization opportunities (Gido et al. 2004) between regions. For example, Ruesink (2005) indicated that invasion success increased with endemism of the native fish fauna, which suggests that invasion success varies regionally because endemism varies regionally.

The drivers of non-native species invasions may also be unclear because most studies evaluated the drivers of non-native species richness and were limited by the assumption that drivers were consistent across species (Lapointe and Light 2012). As a result, species with different functional traits were expected to interact similarly with the environment and native fish assemblage. This assumption, however, may be invalid in some studies because multiple studies across taxa have shown that establishment of non-native species differs between families and based on species characteristics (Kolar and Lodge 2001; Kolar and Lodge 2002; Ruesink 2005). For example, Ruesink (2005) found that establishment was higher for fish species in families with small body size and for omnivores. Given this uncertainty of the primary drivers of non-native fish invasions,

additional research is needed to identify regional and taxonomic differences in the drivers of non-native lotic fish distributions.

To improve our understanding of the drivers of non-native lotic fish establishment, we evaluated the Biotic Resistance, Biotic Acceptance, and Human Activity hypotheses for non-native fishes at the family taxonomic level. The family taxonomic level likely provides more insight into these hypotheses than species richness because phylogenetically similar species possess similar traits (Whitney et al. 2017) and, therefore, likely respond similarly to environmental variability (Frimpong and Angermeier 2010b). This approach is likely particularly informative for evaluating Biotic Resistance and Biotic Acceptance hypotheses because it allows us to examine if native species exclude closely-related non-native species or if they serve as indicators of suitable habitat for closely-related non-native species. Furthermore, evaluating the drivers of non-native fishes at the family taxonomic level is consistent with Lapointe and Light (2012) who indicated that consideration of species identity can improve our understanding of ecosystem invasability, and with Ruesink (2005) who found that establishment was higher for species in families characterized by small body size. Finally, this family-level approach provides generality for predicting species invasions across large spatial extents where the species identity (i.e., species) of potential invaders may be unknown.

Methods

Study Site

We evaluated the Biotic Resistance, Biotic Acceptance, and Human Activity hypotheses for small streams (i.e., 1st – 4th order; USEPA 2005) in the Colorado and

Missouri River basins (CRB and MRB, respectively). These basins provided a unique opportunity to evaluate the drivers of species invasions across a wide range of environmental (e.g. arid to humid, Rocky Mountain to Great Plains terrestrial ecosystems) and fish assemblage (e.g., native and non-native species richness) variability.

The CRB spans approximately 632,000 km² in southwestern USA and northwestern Mexico (Figure 4.1; Carlson and Muth 1989; Olden et al. 2006). The CRB is divided into the upper (UCRB) and lower Colorado River Basin (LCRB) at Glen Canyon Dam, AZ for water management purposes (Olden et al. 2006). The CRB is primarily semi-arid shrub lands and desert shrubs, and the large rivers of the basin flow primarily through highly erodible, sedimentary deposits (Tyus et al. 1982; Blinn and Poff 2005). Mean annual precipitation is 22.1 cm/yr in the UCRB and 10.6 in the LCRB (Blinn and Poff 2005). The CRB is primarily comprised of the Intermountain Plateaus physiographic division, but also contains the Rocky Mountain System physiographic division (Figure 4.1; Fenneman and Johnson 1946). The CRB has a unique fish fauna that consists of 36 native fish species (including 3 marine or brackish species), of which 23 are endemic (Carlson and Muth 1989). However, the distributions and abundances of native fish species have been reduced by altered stream flows, non-native species introductions, reduced water quality, and habitat alteration (Tyus et al. 1982; Carlson and Muth 1989; Valdez and Muth 2005; Kominoski et al. 2018). Approximately 50 non-native species are present in the UCRB (Valdez and Muth 2005). Meanwhile, over 80 non-native species have been introduced to the LCRB, and more than 20 non-native species are relatively common (Minckley and Deacon 1991; Mueller et al. 2005).

The MRB is the second largest river basin in the USA, draining approximately 1,371,017 km² in the USA and 25,100 km² in Canada (Figure 4.1; Galat et al. 2005b). The MRB headwaters originate from the Rocky Mountains at elevations of approximately 1,200 to 4,400 m (Galat et al. 2005a). The MRB is primarily comprised of the semi-arid (36 cm mean annual precipitation) Interior Plains physiographic division, but also includes the Rocky Mountain System (> 80 cm mean annual precipitation) and Interior Highlands (> 100 cm mean annual precipitation) physiographic divisions (Figure 4.1; Fenneman and Johnson 1946; Galat et al. 2005b). The MRB has 138 native and 35 non-native fish species (Galat et al. 2005b). Only two species, the Niangua darter *Etheostoma nianguae* and bluestripe darter *Percina cymatotaenia* are endemic (Cross et al. 1986; Galat et al. 2005b). Although the MRB has been subjected to numerous anthropogenic threats (e.g., land use change, impoundments), the native fish fauna of the MRB has remained relatively intact (Galat et al. 2005b).

Fish Distribution Data

We summarized geo-referenced fish occurrence data for small streams in the CRB and MRB collected between 1990 and 2012. Occurrence data was a compilation of state and federal agency fish collection databases, university and museum collections, and gray literature originally compiled by Annis et al. (2010), Whittier et al. (2011), and Whittier and Sievert (2014). Fish samples were linked to National Hydrography Dataset (NHDPlus Version 1; USEPA and USGS 2005) stream segments using a spatial join in ArcGIS (ESRI 2009). Stream segments are generally lengths of stream between tributary confluences but may be shorter if side channels, divergences, or other features occur (McKay et al. 2012). Samples that did not capture any fish were excluded from our

analysis. All sample records for each stream segment were combined and summarized to native species richness and presence-absence by nativity at the family taxonomic level (e.g., presence-absence of non-native Salmonidae, and presence- absence of native Salmonidae) for our analyses.

Nativity of fish species was determined for each basin and sub-basin based on Cross et al. (1986) for the MRB and Minckley et al. (1986) for the CRB (Appendix 4.1). These sub-basins were the Upper Missouri River, Yellowstone River, White-Little Missouri Rivers, Platte-Niobrara Rivers, James-Sioux Rivers, Chariton-Nishnabotna Rivers, Kansas River, and Lower Missouri River for the MRB, and the UCRB, Middle CRB (MCRB), and LCRB for the CRB (Figure 4.1). We represented the sub-basins from Cross et al. (1986) and Minckley et al. (1986) using 4-digit HUC regions from the NHDplus watershed boundary data layer. We considered the Bill Williams basin part of the LCRB because Minckley et al. (1986) considered most of the Bill Williams basin to be LCRB but indicated that some parts of the basin may be MCRB. Species were assumed to be non-native if they were identified as “uncertain” nativity or omitted by Cross et al. (1986) and Minckley et al. (1986). Subspecies were considered the parent species for nativity assignment and data summarization. We considered the parent species to be native in any sub-basins that a subspecies was native.

Environmental Data

We acquired and summarized landscape-level data of potential anthropogenic disturbances to represent Human Activity Hypothesis independent variables in our analyses. Landscape-level factors were quantified for the upstream watershed (“network” scale) and local catchments (“local” scale) of stream segments. Metrics of human activity

included cultivated crop and urban land uses, dam storage density, dam density, population density, and three disturbance indices (local scale, network scale, and cumulative scale that incorporates disturbances at the local and network scales; Esselman et al. 2011b). Disturbance indices explained the risk of current habitat alteration to fluvial habitats and ranged from 1 (highest risk) to 5 (lowest risk; Esselman et al. 2011a; Esselman et al. 2011b). Values for land use, number of dams, population density, and disturbance indices were acquired from the National Fish Habitat Action Plan (NFHAP) 2010 Habitat Condition Index Scores and Human Disturbance Data for Conterminous United States database (Esselman et al. 2011a). We combined low, medium, and high intensity urban land uses into a total urban land use value. We quantified dam storage density using the Catchment Attribute Allocation and Accumulation Tool (http://www.horizon-systems.com/nhdplus/NHDPlusV1_tools.php) and dam storage data from the 2010 National Inventory of Dams database (USACE 2010). We acquired local catchment and upstream watershed area (km²) values from Esselman et al. (2011a) and calculated dam density as number dams/ area (i.e., catchment or network) and dam storage density as total reservoir storage capacity/ area (i.e., catchment or watershed). We identified correlated human activity metrics using Spearman's correlation analysis and removed metrics that were correlated ($r_s \geq |0.6|$) with other human activity metrics. If a metric type (e.g., crop land use) was strongly correlated between spatial scales (i.e., local, network, cumulative), then we retained the largest spatial scale for analysis.

Data Analysis

We evaluated Biotic Resistance, Biotic Acceptance, and Human Activity hypotheses as drivers of non-native fish family occurrence with logistic regression at five

spatial extents. We used presence-absence by family and nativity (rather than species richness by family and nativity) as our dependent and independent variables because species richness by family and nativity was typically low. The probability of non-native fish family occurrence $[p(x)]$ from the logistic regression model equals $e^{(\alpha + \beta x)} / (1 + e^{(\alpha + \beta x)})$, where α is the intercept, β is the effect of the independent variable on the dependent variable, and x is the independent variable (Agresti 2002). Values of $\beta < 0$ indicate that $p(x)$ decreases as x increases, while values of $\beta > 0$ indicate that $p(x)$ increases as x increases. Therefore, values of $\beta > 0$ would be consistent with the Human Activity Hypothesis for all variables except for the disturbance indices (where values of $\beta < 0$ would be consistent with the hypothesis). However, values of $\beta > 0$ for disturbance metrics and $\beta < 0$ for all other metrics may be consistent with the Human Activity Hypothesis for species intentionally introduced to remote areas (e.g., Adams et al. 2001; Pister 2001). For biotic independent variables (e.g., native species richness), values of $\beta < 0$ suggest biotic resistance, and $\beta > 0$ suggest biotic acceptance. We conducted our analyses at a “global” (i.e., the CRB and MRB combined) spatial extent, and by physiographic division ($n=4$; Fenneman and Johnson 1946; Figure 4.1) to account for the potential effects of large-scale natural environmental factors (e.g., elevation and geology) on the occurrence of fish species that may obscure the drivers of species invasions at large spatial scales.

We evaluated Biotic Resistance, Biotic Acceptance, and Human Activity hypotheses for non-native Salmonidae, Cyprinidae, and Catostomidae. We limited our analysis to these families because they commonly occurred in both basins and have native and non-native representatives in both basins, which was necessary because we

used the presence-absence of native confamilials as metrics representing Biotic Resistance and Biotic Acceptance hypotheses. We also used native species richness to represent Biotic Resistance and Biotic Acceptance hypotheses for all three families, and the presence-absence of native Salmonidae as a metric of Biotic Resistance through predation for non-native Cyprinidae and Catostomidae. We used network crop land use, network human population density, local dam density, network dam density, and cumulative disturbance index as metrics of Human Activity for all families and spatial extents. All of these metrics directly represent potential habitat alteration, while local and network dam density may also directly represent propagule pressure. Furthermore, a negative relationship between non-native species and human activities may represent propagule pressure for non-native species stocked in remote areas (e.g., Adams et al. 2001; Pister 2001). In addition to Biotic Resistance, Biotic Acceptance, and Human Activity hypotheses, we evaluated physiographic division at the global spatial extent to serve as an ecologically relevant null model that accounted for natural environmental variability (e.g., precipitation, latitude, temperature and flow regimes) that may affect fish distributions and abundances across the large study area (Meador et al. 2003; Frimpong and Angermeier 2010a), and a statistical null model at all spatial extents to serve as a baseline for model comparisons.

We compared single-independent variable logistic regression models using Akaike's Information Criterion (AIC) because we were interested in identifying the single best predictor of non-native fish occurrence. The model with the lowest AIC value represented the most-supported model given the data and the models evaluated. Models were ranked according to their ΔAIC values (i.e., $\Delta AIC_{[i]} = AIC \text{ [of model "i"]} - AIC \text{ [of$

most-supported model]). Models with a $\Delta\text{AIC} < 2$ are considered to receive substantial empirical support, while models with ΔAIC between 4 and 7 receive considerably less support, and models with $\Delta\text{AIC} > 10$ have little empirical support (Burnham and Anderson 2002).

We assessed the goodness-of-fit of each model using pseudo- R^2 [McFadden 1974; Agresti 2002; also known as the likelihood ratio R^2 (Menard 2000)], calculated as $(L_0 - L_m)/L_0$, where L_0 is the log-likelihood of the null model and the L_m is the log-likelihood of the model evaluated. This measure is a useful measure for comparing models because it describes the improvement in fit (i.e., reduction in error) relative to the null model and, thus, has similar interpretation as the coefficient of determination in ordinary least squares regression, and is independent of the number of positive outcomes (i.e., non-native family presence; Menard 2000). Models with pseudo- R^2 values between 0.2 and 0.4 are considered to have good fit (McFadden 1979; Hu and Lo 2007), so we only graphically displayed the effect of the independent variable on the dependent variable (i.e., probability of occurrence) for models with a pseudo- R^2 value ≥ 0.2 .

Results

Fish were collected at 6,619 stream segments: 1,589 in the Intermontane Plateaus physiographic division of the CRB, 369 in the Interior Highlands of the MRB, 2,209 in the Interior Plains of the MRB, and 2,452 in the Rocky Mountain System of the CRB (n=1,241) and MRB (n=1,211). Non-native Salmonidae occurred at 1 segment in the Interior Highlands (0.3% of sampled segments), 160 segments (7.2%) in the Interior Plains, 570 segments (35.9%) in the Intermontane Plateaus, and 1,634 segments (66.6%; n=827 in CRB and 807 in MRB) in the Rocky Mountain System physiographic division.

Non-native Cyprinidae occurred at 97 segments (26.3%) in the Interior Highlands, 580 (26.3%) segments in the Interior Plains, 314 segments (19.8%) in the Intermontane Plateaus, and 197 segments (8.0%; n=185 in CRB and 12 in MRB) in the Rocky Mountain System physiographic division. Non-native Catostomidae occurred at 4 segments (1.1%) in the Interior Highlands, 21 segments (1.0%) in the Interior Plains, 66 segments (4.2%) in the Intermontane Plateaus, and 177 segments (7.2%; n=177 in CRB and 0 in MRB) in the Rocky Mountain System physiographic division.

Local scale metrics of human activity were strongly correlated ($p < 0.0001$; $r_s \geq |0.6|$) to their network and cumulative (for disturbance index) scale counterparts for crop land use, human population density, and disturbance index (Table 4.1). Dam density was correlated to dam storage density at both spatial scales. Urban land use was strongly correlated to population density and crop land use at both spatial scales. Finally, local and network disturbance indices were strongly correlated to the cumulative disturbance index. Therefore, we retained local catchment dam density, network crop land use, network population density, network dam density, and cumulative disturbance index as metrics of human activity for our analyses.

The Biotic Resistance, Biotic Acceptance, and Human Activity hypotheses received little support as drivers of non-native Salmonidae presence across spatial extents. At the global spatial extent, the best predictor of non-native Salmonidae presence was physiographic division (pseudo- $R^2=0.26$; Table 4.2; Figure 4.2). Biotic Resistance, Biotic Acceptance, and Human Activity hypotheses did not receive meaningful support ($\Delta AIC > 629$). The most-supported model (network population density) of non-native Salmonidae presence in the Intermontane Plateaus physiographic division of the CRB

represented the Human Activity Hypothesis, and the estimate of β (-0.027; SE=0.012) indicated that the probability of non-native Salmonidae presence decreased with increased population density. The Biotic Acceptance Hypothesis (native Salmonidae) also received meaningful support ($\Delta AIC=5.4$; $\beta=0.46$; SE=0.13), but none of the models for the Intermontane Plateaus explained meaningful variability in non-native Salmonidae presence (pseudo- $R^2 \leq 0.01$). The only supported model for the Interior Plains physiographic division in the MRB represented the Human Activity Hypothesis and indicated the probability of non-native Salmonidae presence decreased with increased network crop land use ($\beta=-0.052$; SE=0.0063), but the model did not explain substantial variability (pseudo- $R^2=0.11$; Table 4.2). The Biotic Resistance Hypothesis (native Salmonidae) was the only model to receive meaningful support in the Rocky Mountain System (CRB and MRB) and indicated the probability non-native Salmonidae occurrence was lower where native Salmonidae occurred ($\beta=-1.47$; SE=0.095; Table 4.2), but this model did not explain significant variability in non-native Salmonidae presence (pseudo- $R^2=0.08$). The drivers of non-native Salmonidae presence were not evaluated for the Interior Highlands physiographic division of the MRB due to a lack of occurrences ($n=1$ of 369 segments).

Biotic Resistance and Biotic Acceptance hypotheses were the most-supported models of non-native Cyprinidae presence across spatial extents, but the most-supported variables differed among regions and generally explained little variability in non-native Cyprinidae presence. The Biotic Acceptance Hypothesis was supported at the global extent, as the probability of non-native Cyprinidae presence increased with native Cyprinidae presence (pseudo- $R^2=0.10$; $\beta=1.92$; SE=0.089; Table 4.3). The other models

did not receive meaningful support ($\Delta AIC > 200$). The Biotic Acceptance Hypothesis was the most-supported model in both the Interior Highlands and Interior Plains physiographic divisions of the MRB because the probability of non-native Cyprinidae presence increased with native species richness (Interior Highlands: $\beta=0.12$, $SE=0.020$; Interior Plains: $\beta=0.11$, $SE=0.0087$), but neither model had good fit ($\text{pseudo-}R^2 \leq 0.10$; Table 4.3). No other variables received meaningful support for either region ($\Delta AIC > 36$; Table 4.3). The Biotic Acceptance Hypothesis was also supported in the Rocky Mountain System of the MRB and CRB because the probability of the non-native Cyprinidae presence was higher at stream segments where native Cyprinidae were also present ($\beta=3.19$; $SE=0.17$; $\text{pseudo-}R^2=0.28$; Table 4.3; Figure 4.2). No other variables received meaningful support for the Rocky Mountain System ($\Delta AIC > 150$; Table 4.3). Finally, the Biotic Resistance Hypothesis was supported for the Intermontane Plateaus of the CRB, as the probability of non-native Cyprinidae presence decreased when native Salmonidae were present ($\beta=-1.95$; $SE=0.30$; $\text{pseudo-}R^2=0.04$; Table 4.3), and other variables did not receive meaningful support ($\Delta AIC > 33$; Table 4.3).

The drivers on non-native Catostomidae presence varied among spatial extents. The Human Activity Hypothesis (network crop land use) was the most-supported model at the global extent, but did not explain significant variability ($\text{pseudo-}R^2=0.03$; Table 4.4). For the Intermontane Plateaus physiographic division of the CRB, the Human Activity (cumulative disturbance index) and Biotic Acceptance (native species richness) hypotheses resulted in the two most-supported models (i.e., non-native Catostomidae presence increased with cumulative disturbance index in the most-supported model and increased with native species richness in the second-most supported model), but neither

model had good model fit ($\text{pseudo-}R^2 \leq 0.07$; Table 4.4). In the Interior Plains of the MRB, the Biotic Acceptance Hypothesis was the only model that received meaningful support and had good model fit ($\text{pseudo-}R^2=0.35$), as the probability of non-native Catostomidae presence increased with native species richness ($\beta=0.28$; $\text{SE}=0.034$; Table 4.4; Figure 4.2). The Biotic Acceptance Hypothesis was the only supported model in the Rocky Mountain System (CRB and MRB), as the probability of non-native Catostomidae presence increased when native Catostomidae were present ($\beta=2.07$; $\text{SE}=0.16$; $\text{pseudo-}R^2=0.11$; Table 4.4). The drivers of non-native Catostomidae presence were not evaluated for the Interior Highlands due to the lack of occurrences ($n=4$ of 369 segments).

Discussion

The drivers of non-native fish invasions varied within and among families and spatial extents, but no obvious patterns across families and extents were present. The best predictor of non-native Salmonidae varied among spatial extents: physiographic division at the global extent, metrics of human activity (potentially representing stocking into remote areas; Adams et al. 2001; Pister et al. 2001) in two physiographic divisions, and Biotic Resistance in one physiographic division. Similarly, the drivers of non-native Cyprinidae varied among extents with support for the Biotic Resistance Hypothesis in one physiographic division and the Biotic Acceptance Hypothesis at the global extent and for three physiographic divisions, but the most-supported metrics of Biotic Acceptance varied among regions. Non-native Catostomidae supported the Human Activity Hypothesis at two extents and the Biotic Acceptance Hypothesis at two extents. Finally, the drivers of non-native lotic fishes generally differed among families within each spatial extent, with an exception being support of the Biotic Acceptance Hypothesis for

non-native Cyprinidae and Catostomidae in two physiographic divisions. Our finding of different drivers of non-native species among families was consistent with Whitney et al. (2017), who found that some non-native families were associated with human activity (i.e., dams), whereas other families were associated with natural abiotic factors (e.g., climate). Similarly, our conclusion of different drivers of non-native species among spatial extents is consistent with Blanchet et al. (2009) who found that the drivers of non-native species richness at the river basin spatial grain differed between their analyses at worldwide and biogeographic region spatial extents. Specifically, these authors found support for the Human Activity Hypothesis at the worldwide extent and the Human Activity and Biotic Acceptance hypotheses when analyses were conducted by biogeographic region.

Spatial grain size of analysis may affect the perceived drivers of species invasions, with more support for Biotic Resistance and Biotic Acceptance hypotheses at smaller spatial grains than at larger spatial grains. At a small spatial grain (i.e., stream segment), we found that metrics representing the Biotic Acceptance Hypothesis were the most-supported variables for 6 of the 13 model sets evaluated and resulted in the only two models representing the hypothesized drivers (excluding physiographic division for non-native Salmonidae) that had good model fit (i.e., $\text{pseudo-}R^2 \geq 0.2$). Meanwhile, the Human Activity Hypothesis was the most-supported hypothesis in four model sets and the Biotic Resistance Hypothesis was the most-supported models in two model sets. Similarly, other studies at small spatial grains (e.g., stream reaches) have provided support for Human Activity (Meador et al. 2003; Gido et al. 2004; Hermoso et al. 2011), Biotic Acceptance (dos Santos et al. 2018), and Biotic Resistance hypotheses (Fitzgerald

et al. 2016). Unlike these studies at small spatial grains, studies at larger spatial grain sizes (e.g., river basin) almost exclusively provided support for the Human Activity Hypothesis (Gido et al. 2004; Light and Marchetti 2007; Leprieur et al. 2008; Blanchet et al. 2009; Copp et al. 2010; Lapointe and Light 2012; Pool et al. 2010), although Blanchet et al. (2009) provided support for the Biotic Acceptance Hypothesis in some regions. The greater support for biotic interactions structuring fish assemblages at small spatial grains than at large spatial grains is consistent with Tonn (1990), Poff (1997), Jackson et al. (2001), and Fitzgerald et al. (2016), who suggested that biotic interactions are more likely to structure fish assemblages at small scales (i.e., grain) than at larger spatial scales.

Natural environmental factors (e.g., climate, geology, and in-stream habitat) may be more important drivers of non-native fish occurrence at the stream segment spatial grain than metrics human activity or interactions with the native fish assemblage for the spatial extents evaluated in this study. Most model sets in our study (10 of 13 family-region combinations) did not contain models with good fit (i.e., $\text{psuedo-}R^2 \geq 0.2$), suggesting that human activities and the native fish assemblage may not be the primary drivers of non-native Salmonidae, Catostomidae, and Cyprinidae presence. Furthermore, one of the models with good fit (i.e., non-native Salmonidae global extent model set) indicated that natural environmental variability (i.e., physiographic division) was a better predictor of non-native Salmonidae occurrence than metrics of human activity or the native fish assemblage, but this result may also reflect variability in propagule pressure among physiographic divisions (e.g., more non-native trout stockings in the Rocky Mountain System relative to other regions). The hypothesis that natural environmental factors are primary drivers of species invasions at this spatial scale is consistent with

Pierce (2019; Chapter 3; MRB and CRB) and Whitney et al. (2017; upper CRB), who found that natural environmental factors were often important predictors of non-native species occurrences, though non-native Cyprinidae and families not evaluated in this study were also associated with dams in the upper CRB (Whitney et al. 2017).

Furthermore, natural factors (e.g., watershed area, climatic factors, and hydrological regime) were identified as important predictors of non-native species invasion success (Moyle and Light 1996), density (Propst et al. 2008), richness (Gido and Brown 1999; Gido et al. 2004; Light and Marchetti 2007; Blanchet et al. 2009), functional diversity (Pool et al. 2010), and species composition (Pool et al. 2010; Lapointe and Light 2012) at multiple spatial grains.

Considering non-native species invasions within the context of hierarchical habitat filters (Tonn 1990; Poff 1997; Jackson et al. 2001) may provide clarity on the context-dependent nature (Blanchet et al. 2009; e.g., vary by species, spatial extent, and spatial grain) of the drivers of species invasions. From the hierarchical habitat filtering perspective, non-native species establishment can be viewed as a stepwise process: 1) species introduced to new area, bypassing biogeographical filters; 2) environmental filters determine potential distribution within introduced range; and 3) biotic interactions determine realized distribution within potential distribution. Therefore, in order for mechanisms to drive non-native species establishment at steps 2 or 3, the preceding step(s) may need to be satisfied. For example, it may be unwarranted to conclude that biotic interactions (e.g., Biotic Resistance Hypothesis) prevented the establishment of a non-native species that was not introduced or was introduced to an area without suitable abiotic conditions (e.g., thermal regime). This invasion process may explain variability in

the drivers of invasion among spatial scales. The presence of a non-native species in a region is first dependent on human introductions (i.e., Step 1), suggesting the Human Activity Hypothesis should be supported at large spatial scales. Meanwhile, intermediate spatial scales may relate to Step 2 in the invasion process, with non-native species distributions dependent on natural (potentially supporting Biotic Acceptance Hypothesis as a surrogate for intermediate-scale habitat quality) or anthropogenic environmental factors (i.e., Human Activity Hypothesis). At the smallest spatial scales, the Biotic Acceptance (as a surrogate for fine-scale habitat quality) or Biotic Resistance (i.e., negative species interactions) hypotheses may explain non-native species occurrence. Finally, the proposed hierarchical habitat filtering process highlights the need to evaluate the drivers of species invasions at the species taxonomic level because the means (e.g., stocking or unintentional) and spatial extent of introductions (i.e., Step 1), environmental needs (i.e., Step 2), and potential biotic interactions (i.e., Step 3) likely vary among species.

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Tables

Table 4.1. Spearman rank correlation (r_s) of landscape-level metrics of human activity for 1st to 4th order stream segments in the Missouri and Colorado River basins where fish were collected for this study. The top value represents r_s and the bottom value represents the p -value for each correlation. Values in bold indicate strong ($r_s \geq |0.6|$) correlations. Prefixes “L_”, “N_”, and “C_” represent local catchment, network watershed, and cumulative spatial scales, respectively, of landscape-level environmental data.

	L_Population density	N_Crop land use	N_Population density	L_Disturbance index	N_Disturbance index	C_Disturbance index	L_Dam density	N_Dam density	L_Dam storage density	N_Dam storage density	L_Urban land use	N_Urban land use
L_Crop land use	0.463 <0.0001	0.859 <0.0001	0.473 <0.0001	-0.491 <0.0001	-0.497 <0.0001	-0.500 <0.0001	0.177 <0.0001	0.375 <0.0001	0.176 <0.0001	0.327 <0.0001	0.612 <0.0001	0.661 <0.0001
L_Population density		0.462 <0.0001	0.908 <0.0001	-0.558 <0.0001	-0.523 <0.0001	-0.520 <0.0001	0.144 <0.0001	0.297 <0.0001	0.144 <0.0001	0.289 <0.0001	0.627 <0.0001	0.633 <0.0001
N_Crop land use			0.501 <0.0001	-0.509 <0.0001	-0.574 <0.0001	-0.566 <0.0001	0.173 <0.0001	0.449 <0.0001	0.172 <0.0001	0.401 <0.0001	0.632 <0.0001	0.729 <0.0001
N_Population density				-0.521 <0.0001	-0.572 <0.0001	-0.538 <0.0001	0.140 <0.0001	0.336 <0.0001	0.140 <0.0001	0.322 <0.0001	0.601 <0.0001	0.695 <0.0001
L_Disturbance index					0.657 <0.0001	0.799 <0.0001	-0.156 <0.0001	-0.313 <0.0001	-0.156 <0.0001	-0.306 <0.0001	-0.627 <0.0001	-0.581 <0.0001
N_Disturbance index						0.925 <0.0001	-0.243 <0.0001	-0.598 <0.0001	-0.243 <0.0001	-0.568 <0.0001	-0.562 <0.0001	-0.670 <0.0001
C_Disturbance index							-0.237 <0.0001	-0.570 <0.0001	-0.237 <0.0001	-0.544 <0.0001	-0.580 <0.0001	-0.637 <0.0001
L_Dam density								0.329 <0.0001	1.000 <0.0001	0.293 <0.0001	0.150 <0.0001	0.167 <0.0001
N_Dam density									0.329 <0.0001	0.966 <0.0001	0.372 <0.0001	0.454 <0.0001
L_Dam storage density										0.293 <0.0001	0.150 <0.0001	0.166 <0.0001
N_Dam storage density											0.354 <0.0001	0.429 <0.0001
L_Urban land use												0.817 <0.0001

Table 4.2. Logistic regression model results for Human Activity, Biotic Resistance, and Biotic Acceptance hypotheses predicting non-native Salmonidae presence in the Missouri and Colorado River basins. Interior Highlands was excluded from analysis by physiographic division due to low sample size. k=number of model parameters.

Spatial Extent	Variable	Hypothesis	AIC	Δ AIC	k	Deviance	Pseudo- R^2
Global	Physiographic division	Natural	6366.6	0.0	4	6358.6	0.26
	Native species richness	Biotic Acceptance/ Resistance	6996.1	629.5	2	6992.1	0.19
	Network crop land use	Human Activity	7348.4	981.8	2	7344.4	0.15
	Network population density	Human Activity	8210.6	1844.0	2	8206.6	0.05
	Cumulative disturbance	Human Activity	8317.3	1950.7	2	8313.3	0.04
	Native Salmonidae	Biotic Acceptance/ Resistance	8425.5	2058.9	2	8421.5	0.02
	Network dam density	Human Activity	8486.5	2119.9	2	8482.5	0.02
	Local catchment dam density	Human Activity	8616.7	2250.1	2	8612.7	0.00
	Null		8631.2	2264.6	1	8629.2	0.00
134	Interior Highlands	N/A					
	Intermontane Plateaus	Network population density	2060.7	0.0	2	2056.7	0.01
		Native Salmonidae	2066.1	5.4	2	2062.1	0.01
		Cumulative disturbance	2067.1	6.4	2	2063.1	0.01
		Network dam density	2068.2	7.5	2	2064.2	0.00
		Null	2076.2	15.5	1	2074.2	0.00
		Network crop land use	2078.1	17.4	2	2074.1	0.00
		Local catchment dam density	2078.2	17.5	2	2074.2	0.00
		Native species richness	2078.2	17.5	2	2074.2	0.00
	Interior Plains	Network crop land use	1026.1	0.0	2	1022.1	0.11
		Network dam density	1061.2	35.1	2	1057.2	0.08
		Native Salmonidae	1066.9	40.8	2	1062.9	0.07
		Native species richness	1080.5	54.4	2	1076.5	0.06
		Cumulative disturbance	1089.0	62.9	2	1085.0	0.06
		Network population density	1097.3	71.2	2	1093.3	0.05

Spatial Extent	Variable	Hypothesis	AIC	Δ AIC	k	Deviance	Pseudo- R^2
	Local catchment dam density	Human Activity	1142.3	116.2	2	1138.3	0.01
	Null		1150.2	124.1	1	1148.2	0.00
Rocky Mountain System	Native Salmonidae	Biotic Acceptance/ Resistance	2862.4	0.0	2	2858.4	0.08
	Native species richness	Biotic Acceptance/ Resistance	2992.7	130.3	2	2988.7	0.04
	Cumulative disturbance	Human Activity	3106.1	243.7	2	3102.1	0.01
	Network population density	Human Activity	3117.8	255.4	2	3113.8	0.00
	Null		3124.4	262.0	1	3122.4	0.00
	Network crop land use	Human Activity	3125.1	262.7	2	3121.1	0.00
	Network dam density	Human Activity	3125.6	263.2	2	3121.6	0.00
	Local catchment dam density	Human Activity	3125.9	263.5	2	3121.9	0.00

Table 4.3. Logistic regression model results for Human Activity, Biotic Resistance, and Biotic Acceptance hypotheses predicting non-native Cyprinidae presence in the Missouri and Colorado River basins. k=number of model parameters.

Spatial Extent	Variable	Hypothesis	AIC	Δ AIC	k	Deviance	Pseudo- R^2
Global	Native Cyprinidae	Biotic Acceptance/ Resistance	5597.4	0.0	2	5593.4	0.10
	Native species richness	Biotic Acceptance/ Resistance	5806.3	208.9	2	5802.3	0.07
	Native Salmonidae	Biotic Acceptance/ Resistance	5858.1	260.7	2	5854.1	0.06
	Physiographic division	Natural	5927.5	330.1	4	5919.5	0.05
	Cumulative disturbance	Human Activity	6027.1	429.7	2	6023.1	0.03
	Network crop land use	Human Activity	6049.9	452.5	2	6045.9	0.03
	Network dam density	Human Activity	6222.1	624.7	2	6218.1	0.00
	Local catchment dam density	Human Activity	6230.5	633.1	2	6226.5	0.00
	Network population density	Human Activity	6231.7	634.3	2	6227.7	0.00
	Null		6231.9	634.5	1	6229.9	0.00
136 Interior Highlands	Native species richness	Biotic Acceptance/ Resistance	384.9	0.0	2	380.9	0.10
	Network crop land use	Human Activity	421.1	36.1	2	417.1	0.02
	Native Cyprinidae	Biotic Acceptance/ Resistance	423.6	38.6	2	419.6	0.01
	Null		427.1	42.2	1	425.1	0.00
	Native Salmonidae	Biotic Acceptance/ Resistance	427.1	42.2	2	423.1	0.00
	Local catchment dam density	Human Activity	428.1	43.2	2	424.1	0.00
	Network population density	Human Activity	428.9	44.0	2	424.9	0.00
	Network dam density	Human Activity	429.0	44.1	2	425.0	0.00
	Cumulative disturbance	Human Activity	429.0	44.1	2	425.0	0.00
Intermontane Plateaus	Native Salmonidae	Biotic Acceptance/ Resistance	1512.7	0.0	2	1508.7	0.04
	Cumulative disturbance	Human Activity	1546.6	33.9	2	1542.6	0.02
	Native Cyprinidae	Biotic Acceptance/ Resistance	1547.3	34.6	2	1543.3	0.02
	Native species richness	Biotic Acceptance/ Resistance	1547.5	34.8	2	1543.5	0.02
	Network crop land use	Human Activity	1576.5	63.8	2	1572.5	0.00
	Null		1581.7	69.0	1	1579.7	0.00
	Network dam density	Human Activity	1583.5	70.8	2	1579.5	0.00

Spatial Extent	Variable	Hypothesis	AIC	Δ AIC	k	Deviance	Pseudo- R^2
	Local catchment dam density	Human Activity	1583.6	70.9	2	1579.6	0.00
	Network population density	Human Activity	1583.7	71.0	2	1579.7	0.00
Interior Plains	Native species richness	Biotic Acceptance/ Resistance	2378.8	0.0	2	2374.8	0.07
	Network crop land use	Human Activity	2507.5	128.7	2	2503.5	0.02
	Native Cyprinidae	Biotic Acceptance/ Resistance	2516.0	137.2	2	2512.0	0.01
	Native Salmonidae	Biotic Acceptance/ Resistance	2536.8	158.0	2	2532.8	0.00
	Cumulative disturbance	Human Activity	2541.9	163.1	2	2537.9	0.00
	Null		2545.5	166.7	1	2543.5	0.00
	Local catchment dam density	Human Activity	2545.6	166.8	2	2541.6	0.00
	Network dam density	Human Activity	2547.5	168.7	2	2543.5	0.00
	Network population density	Human Activity	2547.5	168.7	2	2543.5	0.00
Rocky Mountain System	Native Cyprinidae	Biotic Acceptance/ Resistance	996.9	0.0	2	992.9	0.28
	Native species richness	Biotic Acceptance/ Resistance	1147.6	150.7	2	1143.6	0.17
	Native Salmonidae	Biotic Acceptance/ Resistance	1297.3	300.4	2	1293.3	0.06
	Cumulative disturbance	Human Activity	1312.9	316.0	2	1308.9	0.05
	Local catchment dam density	Human Activity	1369.2	372.3	2	1365.2	0.00
	Network dam density	Human Activity	1370.6	373.7	2	1366.6	0.00
	Null		1373.2	376.3	1	1371.2	0.00
	Network crop land use	Human Activity	1374.6	377.7	2	1370.6	0.00
	Network population density	Human Activity	1375.0	378.1	2	1371.0	0.00

Table 4.4. Logistic regression model results for Human Activity, Biotic Resistance, and Biotic Acceptance hypotheses predicting non-native Catostomidae presence in the Missouri and Colorado River basins. Interior Highlands was excluded from analysis by physiographic division due to low sample size. k=number of model parameters.

Spatial Extent	Variable	Hypothesis	AIC	Δ AIC	k	Deviance	Pseudo- R^2
Global	Network crop land use	Human Activity	2176.1	0.0	2	2172.1	0.03
	Native Catostomidae	Biotic Acceptance/ Resistance	2183.6	7.5	2	2179.6	0.03
	Physiographic division	Natural	2210.0	33.9	4	2202.0	0.02
	Cumulative disturbance	Human Activity	2223.9	47.8	2	2219.9	0.01
	Native Salmonidae	Biotic Acceptance/ Resistance	2243.6	67.5	2	2239.6	0.00
	Null		2245.8	69.7	1	2243.8	0.00
	Network population density	Human Activity	2246.2	70.1	2	2242.2	0.00
	Network dam density	Human Activity	2246.8	70.7	2	2242.8	0.00
	Native species richness	Biotic Acceptance/ Resistance	2247.5	71.4	2	2243.5	0.00
	Local catchment dam density	Human Activity	2247.8	71.7	2	2243.8	0.00
Interior Highlands	N/A						
Intermontane Plateaus	Cumulative disturbance	Human Activity	517.4	0.0	2	513.4	0.07
	Native species richness	Biotic Acceptance/ Resistance	521.9	4.5	2	517.9	0.06
	Native Catostomidae	Biotic Acceptance/ Resistance	525.0	7.6	2	521.0	0.05
	Network crop land use	Human Activity	539.8	22.4	2	535.8	0.02
	Local catchment dam density	Human Activity	550.7	33.4	2	546.7	0.00
	Null		551.1	33.8	1	549.1	0.00
	Network dam density	Human Activity	552.7	35.3	2	548.7	0.00
	Native Salmonidae	Biotic Acceptance/ Resistance	552.7	35.3	2	548.7	0.00
	Network population density	Human Activity	553.0	35.6	2	549.0	0.00
Interior Plains	Native species richness	Biotic Acceptance/ Resistance	157.9	0.0	2	153.9	0.35
	Native Catostomidae	Biotic Acceptance/ Resistance	215.5	57.6	2	211.5	0.11
	Network crop land use	Human Activity	230.2	72.3	2	226.2	0.05
	Null		239.3	81.4	1	237.3	0.00

Spatial Extent	Variable	Hypothesis	AIC	Δ AIC	k	Deviance	Pseudo- R^2
	Cumulative disturbance	Human Activity	240.2	82.3	2	236.2	0.00
	Network dam density	Human Activity	240.5	82.6	2	236.5	0.00
	Native Salmonidae	Biotic Acceptance/ Resistance	240.7	82.8	2	236.7	0.00
	Network population density	Human Activity	241.0	83.1	2	237.0	0.00
	Local catchment dam density	Human Activity	241.3	83.4	2	237.3	0.00
Rocky Mountain System	Native Catostomidae	Biotic Acceptance/ Resistance	1130.1	0.0	2	1126.1	0.11
	Native species richness	Biotic Acceptance/ Resistance	1185.7	55.6	2	1181.7	0.07
	Cumulative disturbance	Human Activity	1202.1	72.0	2	1198.1	0.06
	Native Salmonidae	Biotic Acceptance/ Resistance	1210.0	79.9	2	1206.0	0.05
	Network population density	Human Activity	1256.0	125.9	2	1252.0	0.02
	Network dam density	Human Activity	1257.3	127.2	2	1253.3	0.01
	Local dam density	Human Activity	1258.7	128.6	2	1254.7	0.01
	Null		1273.4	143.3	1	1271.4	0.00
	Network crop land use	Human Activity	1275.4	145.3	2	1271.4	0.00

Figures

Figure 4.1. Physiographic divisions (top; Fenneman and Johnson 1946) and biogeographical regions of the Missouri and Colorado River basins (MRB and CRB, respectively). Biogeographic regions were adapted from Cross et al. (1986) for the MRB and Minckley et al. (1986) for the CRB.

Figure 4.2. Predicted probability of non-native Salmonidae occurrence by physiographic division estimated from logistic regression at the global spatial extent (top), predicted probability of non-native Cyprinidae occurrence by native Cyprinidae occurrence in the Rocky Mountain System physiographic division (middle), and predicted probability of non-native Catostomidae occurrence as a function of native species richness in the Interior Plains physiographic division (bottom).

Appendices

Appendix 4.1. Species occurrence (number of stream segments) and nativity by biogeographic region. An asterisk (*) indicates species that were considered non-native based on Minckley et al. (1986) for the Colorado River basin and Cross et al. (1986) for the Missouri River basin. Biogeographic region abbreviations represent Chariton-Nishnabotna (CN), Kansas (KS), Lower Missouri (LM), Platte-Niobrara (PN), Sioux-James (SJ), Upper Missouri (UM), White-Little Missouri (WL), Yellowstone (YS), Lower Colorado River Basin (LC), Middle Colorado River Basin (MC), and Upper Colorado River Basin (UC).

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Common name	Scientific name	Family	Missouri River biogeographic region								Colorado River biogeographic region		
			CN	KS	LM	PN	SJ	UM	WL	YS	LC	MC	UC
Alewife	<i>Alosa pseudoharengus</i>	Clupeidae				1*							
Arctic Grayling	<i>Thymallus arcticus</i>	Salmonidae						29			1*	1*	
Ash Meadows	<i>Cyprinodon nevadensis</i>	Cyprinodontidae										7*	
Amargosa Pupfish	<i>mionectes</i>												
Banded Darter	<i>Etheostoma zonale</i>	Percidae			36								
Banded Sculpin	<i>Cottus carolinae</i>	Cottidae			67								
Bigeye Shiner	<i>Notropis boops</i>	Cyprinidae			43								
Bighead Carp	<i>Hypophthalmichthys nobilis</i>	Cyprinidae	3*		5*	1*							
Bigmouth Buffalo	<i>Ictiobus cyprinellus</i>	Catostomidae	22		21	2				1			
Bigmouth Shiner	<i>Notropis dorsalis</i>	Cyprinidae	429	17	77	96	27		1				1*
Black Buffalo	<i>Ictiobus niger</i>	Catostomidae	2		3								
Black Bullhead	<i>Ameiurus melas</i>	Ictaluridae	165	68	121	64	14	47*	36	70*	14*	2*	17*
Black Crappie	<i>Pomoxis nigromaculatus</i>	Centrarchidae	18*	4*	26	3*			2*	3*	1*		6*
Black Redhorse	<i>Moxostoma duquesnei</i>	Catostomidae	1*		93								
Blacknose Shiner	<i>Notropis heterolepis</i>	Cyprinidae			34								
Blackside Darter	<i>Percina maculata</i>	Percidae	17	2	9		1						
Blackspotted Topminnow	<i>Fundulus olivaceus</i>	Fundulidae			183								
Blackstripe Topminnow	<i>Fundulus notatus</i>	Fundulidae	1*		122								
Blacktail Shiner	<i>Cyprinella venusta</i>	Cyprinidae			9*								
Bleeding Shiner	<i>Luxilus zonatus</i>	Cyprinidae			226								
Blue Tilapia	<i>Oreochromis aureus</i>	Cichlidae									1*		
Bluegill	<i>Lepomis macrochirus</i>	Centrarchidae	323*	61*	560	48*	7*				12*	1*	9*
Bluehead Sucker	<i>Catostomus discobolus</i>	Catostomidae									1*	94	180

Common name	Scientific name	Family	Missouri River biogeographic region								Colorado River biogeographic region		
			CN	KS	LM	PN	SJ	UM	WL	YS	LC	MC	UC
Bluestripe Darter	<i>Percina cymatotaenia</i>	Percidae			6								
Bluntnose Minnow	<i>Pimephales notatus</i>	Cyprinidae	233	30	480		2						
Bonytail Chub	<i>Gila elegans</i>	Cyprinidae									3		2
Brassy Minnow	<i>Hybognathus hankinsoni</i>	Cyprinidae	60	10		9	1	96	11	44			
Brook Silverside	<i>Labidesthes sicculus</i>	Atherinopsidae	5*	1*	191	4*							
Brook Stickleback	<i>Culaea inconstans</i>	Gasterosteidae	13*			2	2	131	10	55			11*
Brook Trout	<i>Salvelinus fontinalis</i>	Salmonidae		1*		7*		626*	8*	56*	3*	26*	754*
Brown Trout	<i>Salmo trutta</i>	Salmonidae		3*		50*		119*	16*	83*	58*	55*	459*
Bull Trout	<i>Salvelinus confluentus</i>	Salmonidae						7*					
Bullhead Minnow	<i>Pimephales vigilax</i>	Cyprinidae		7*	4*								
Burbot	<i>Lota lota</i>	Gadidae						26		1			
Cardinal Shiner	<i>Luxilus cardinalis</i>	Cyprinidae			1*								
Carmine Shiner	<i>Notropis percobromus</i>	Cyprinidae		12*	100*								
Central Stoneroller	<i>Campostoma anomalum</i>	Cyprinidae	345	70	579	35	4		4				
Channel Catfish	<i>Ictalurus punctatus</i>	Ictaluridae	167	34	84	41	16	5	4	45	4*	7*	7*
Chestnut Lamprey	<i>Ichthyomyzon castaneus</i>	Petromyzontidae			1								
Colorado Pikeminnow	<i>Ptychocheilus lucius</i>	Cyprinidae											10
Common Carp	<i>Cyprinus carpio</i>	Cyprinidae	110*	45*	91*	75*	16*	85*	12*	84*	16*	7*	21*
Common Shiner	<i>Luxilus cornutus</i>	Cyprinidae	75	26	178	7	3		1				
Convict Cichlid	<i>Amatitlania nigrofasciata</i>	Cichlidae										2*	
Creek Chub	<i>Semotilus atromaculatus</i>	Cyprinidae	490	70	532	165	30	8*	28	78			75*
Cutthroat Trout	<i>Oncorhynchus clarkii</i>	Salmonidae						577		99	1*	11*	742
Desert Pupfish	<i>Cyprinodon macularius</i>	Cyprinodontidae									24		
Desert Sucker	<i>Catostomus clarkii</i>	Catostomidae									243	28	
Devils Hole Pupfish	<i>Cyprinodon diabolis</i>	Cyprinodontidae										2*	
Emerald Shiner	<i>Notropis atherinoides</i>	Cyprinidae	20	3	10	4	6	6	1	17			
Fantail Darter	<i>Etheostoma flabellare</i>	Percidae	1*		263								
Fathead Minnow	<i>Pimephales promelas</i>	Cyprinidae	407	93	87	174	36	315	65	225	69*	90*	146*
Finescale Dace	<i>Phoxinus neogaeus</i>	Cyprinidae				1							
Flannelmouth Sucker	<i>Catostomus latipinnis</i>	Catostomidae									2	14	143
Flathead Catfish	<i>Pylodictis olivaris</i>	Ictaluridae	22	11	19	2	1				5*		
Flathead Chub	<i>Platygobio gracilis</i>	Cyprinidae	18					37	3	80			
Freckled Madtom	<i>Noturus nocturnus</i>	Ictaluridae			1								
Freshwater Drum	<i>Aplodinotus grunniens</i>	Sciaenidae	20	7	28	7	4						
Ghost Shiner	<i>Notropis buchanani</i>	Cyprinidae	2		6								
Gila Chub	<i>Gila intermedia</i>	Cyprinidae									73	1*	
Gila Topminnow	<i>Poeciliopsis occidentalis</i>	Poeciliidae									114		
Gila Trout	<i>Oncorhynchus gilae</i>	Salmonidae									76	8	
Gizzard Shad	<i>Dorosoma cepedianum</i>	Clupeidae	28	6	69	7	4						

Common name	Scientific name	Family	Missouri River biogeographic region								Colorado River biogeographic region		
			CN	KS	LM	PN	SJ	UM	WL	YS	LC	MC	UC
Golden Redhorse	Moxostoma erythrurum	Catostomidae	3	10*	148								
Golden Shiner	Notemigonus crysoleucas	Cyprinidae	60	7	131	5		6*	8*	1*		13*	
Golden Topminnow	Fundulus chrysotus	Fundulidae			1*								
Goldeye	Hiodon alosoides	Hiodontidae	6		3		1	4	1	10			
Goldfish	Carassius auratus	Cyprinidae	4*		4*						4*		1*
Grass Carp	Ctenopharyngodon idella	Cyprinidae	1*		5*	2*					2*		1*
Grass Pickerel	Esox americanus	Esocidae					13						
Gravel Chub	Erimystax x-punctatus	Cyprinidae			2								
Green Sunfish	Lepomis cyanellus	Centrarchidae	423	99	595	117	17	11*	39*	78*	111*	21*	33*
Greenside Darter	Etheostoma blennioides	Percidae			138								
Guppy	Poecilia reticulata	Poeciliidae									1*		
Headwater Chub	Gila nigra	Cyprinidae									34		
Highfin Carpsucker	Carpododes velifer	Catostomidae	1										
Hornyhead Chub	Nocomis biguttatus	Cyprinidae	5*		122	3							
Humpback Chub	Gila cypha	Cyprinidae										4	
Iowa Darter	Etheostoma exile	Percidae	2*			13	1	37	7				2*
Johnny Darter	Etheostoma nigrum	Percidae	222	49	207	14	7		3*				1*
Kokanee	Oncorhynchus nerka	Salmonidae											18*
Lake Chub	Couesius plumbeus	Cyprinidae				1		183	5	141			13*
Lake Trout	Salvelinus namaycush	Salmonidae											5*
Largemouth Bass	Micropterus salmoides	Centrarchidae	274	53	455	54	4	2*	1*	2*	28*	11*	10*
Largescale Stoneroller	Camptostoma oligolepis	Cyprinidae			161								
Least Darter	Etheostoma microperca	Percidae			13								
Little Colorado Spinedace	Lepidomeda vittata	Cyprinidae										36	
Little Colorado Sucker	Catostomus sp.	Catostomidae										45	
Loach Minnow	Rhinichthys cobitis	Cyprinidae									33		
Logperch	Percina caprodes	Percidae	4*	14	230								
Longear Sunfish	Lepomis megalotis	Centrarchidae	2*	12*	328								
Longfin Dace	Agosia chrysogaster	Cyprinidae											
Longnose Dace	Rhinichthys cataractae	Cyprinidae				101	9*	159	32	177	321	1*	39*
Longnose Gar	Lepisosteus osseus	Lepisosteidae	10	4	31	2							
Longnose Sucker	Catostomus catostomus	Catostomidae				27		65	2	72			70*
Mexican Stoneroller	Camptostoma ornatum	Cyprinidae									4*		
Mimic Shiner	Notropis volucellus	Cyprinidae			2								
Missouri Saddled Darter	Etheostoma tetrazonum	Percidae			23								
Mottled Sculpin	Cottus bairdii	Cottidae			71			106*		25*			546
Mountain Madtom	Noturus eleutherus	Ictaluridae			1*								

Common name	Scientific name	Family	Missouri River biogeographic region								Colorado River biogeographic region		
			CN	KS	LM	PN	SJ	UM	WL	YS	LC	MC	UC
Mountain Sucker	Catostomus platyrhynchus	Catostomidae						47	2	67			247
Mountain Whitefish	Prosopium williamsoni	Salmonidae						26		18			79
Mozambique Tilapia	Tilapia mossambica	Cichlidae									1*		
Niangua Darter	Etheostoma nianguae	Percidae			15								
Northern Brook Lamprey	Ichthyomyzon fossor	Petromyzontidae			1								
Northern Hog Sucker	Hypentelium nigricans	Catostomidae			124								
Northern Leatherside Chub	Lepidomeda copei	Cyprinidae											6*
Northern Pike	Esox lucius	Esocidae	8*			5		37*	12	7*			
Northern Plains Killifish	Fundulus kansae	Fundulidae		17*	10*	8*		9*	7*	63*			
Northern Redbelly Dace	Phoxinus eos	Cyprinidae						100		9			
Northern Studfish	Fundulus catenatus	Fundulidae			169								
Orangespotted Sunfish	Lepomis humilis	Centrarchidae	81	26	102	4	2		4				
Orangethroat Darter	Etheostoma spectabile	Percidae	5	35	599								
Ozark Minnow	Notropis nubilus	Cyprinidae			188								
Ozark Sculpin	Cottus hypselurus	Cottidae			33*								
Paddlefish	Polyodon spathula	Polyodontidae			2								
Pahrump Killifish	Empetrichthys latos	Goodeidae										2*	
Paiute Sculpin	Cottus beldingii	Cottidae											15
Pealip Redhorse	Moxostoma pisolabrum	Catostomidae			8*								
Pearl Dace	Margariscus margarita	Cyprinidae				1		12					
Plains Killifish	Fundulus zebrinus	Fundulidae										7*	7*
Plains Minnow	Hybognathus placitus	Cyprinidae	9	2	1			53	4	60			
Plains Topminnow	Fundulus sciadicus	Fundulidae			53	7			2				
Pumpkinseed	Lepomis gibbosus	Centrarchidae	1*	1*		5*		3*		8*			
Quillback	Carpionodes cyprinus	Catostomidae	72	8	19	14	4						
Quitobquito Pupfish	Cyprinodon eremus	Cyprinodontidae									1*		
Rainbow Darter	Etheostoma caeruleum	Percidae			147								
Rainbow Trout	Oncorhynchus mykiss	Salmonidae		4*	1*	29*		249*	4*	28*	85*	93*	535*
Razorback Sucker	Xyrauchen texanus	Catostomidae									6		2
Red Shiner	Cyprinella lutrensis	Cyprinidae	413	94	352	99	13		2		51*	11*	20*
Redbelly Tilapia	Tilapia zillii	Cichlidae									3*		
Redear Sunfish	Lepomis microlophus	Centrarchidae		2*	24*	1*					4*		
Redfin Shiner	Lythrurus umbratilis	Cyprinidae	93	19	333								
Redside Shiner	Richardsonius balteatus	Cyprinidae											75*
Ribbon Shiner	Lythrurus fumeus	Cyprinidae			1*								

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			CN	KS	LM	PN	SJ	UM	WL	YS	LC	MC	UC
Rio Grande Chub	<i>Gila pandora</i>	Cyprinidae											2*
Rio Grande Cichlid	<i>Herichthys cyanoguttatus</i>	Cichlidae										1*	
Rio Grande Sucker	<i>Catostomus plebeius</i>	Catostomidae									2*		
River Carpsucker	<i>Carpionodes carpio</i>	Catostomidae	115	11	31	29	4	13		39			
River Shiner	<i>Notropis blennius</i>	Cyprinidae	5	2		18	2						1*
Rock Bass	<i>Ambloplites rupestris</i>	Centrarchidae		1*	34*	2*			1*				
Roundtail Chub	<i>Gila robusta</i>	Cyprinidae									79	8	61
Sailfin Molly	<i>Poecilia latipinna</i>	Poeciliidae										1*	
Sand Shiner	<i>Notropis stramineus</i>	Cyprinidae	423	65	269	164	33	31*	25	88			19*
Sauger	<i>Sander canadensis</i>	Percidae	2		1			1		1			
Shoal Chub	<i>Macrhybopsis hyostoma</i>	Cyprinidae	2			2							
Shortfin Molly	<i>Poecilia mexicana</i>	Poeciliidae										2*	
Shorthead Redhorse	<i>Moxostoma macrolepidotum</i>	Catostomidae	43	10	23	28	11	15	6	50			
Shortnose Gar	<i>Lepisosteus platostomus</i>	Lepisosteidae	21		28	2	4		1				
Silver Carp	<i>Hypophthalmichthys molitrix</i>	Cyprinidae	4*		1*								
Silver Chub	<i>Macrhybopsis storeriana</i>	Cyprinidae	11		2								
Silver Redhorse	<i>Moxostoma anisurum</i>	Catostomidae			13								
Slender Madtom	<i>Noturus exilis</i>	Ictaluridae	1	14	249								
Slenderhead Darter	<i>Percina phoxocephala</i>	Percidae	1*	1*	30								
Slough Darter	<i>Etheostoma gracile</i>	Percidae			4								
Smallmouth Bass	<i>Micropterus dolomieu</i>	Centrarchidae			91	3*	1*	3*		3*	20*		13*
Smallmouth Buffalo	<i>Ictiobus bubalus</i>	Catostomidae	9		17			1		1			
Sonora Chub	<i>Gila ditaenia</i>	Cyprinidae									12*		
Sonora Sucker	<i>Catostomus insignis</i>	Catostomidae									130		
Southern Redbelly Dace	<i>Phoxinus erythrogaster</i>	Cyprinidae	7*	26	137								
Speckled Dace	<i>Rhinichthys osculus</i>	Cyprinidae									256	143	467
Spikedace	<i>Meda fulgida</i>	Cyprinidae									2		
Spotfin Shiner	<i>Cyprinella spiloptera</i>	Cyprinidae	6*										
Spottail Shiner	<i>Notropis hudsonius</i>	Cyprinidae					1	17*		1*			
Spotted Bass	<i>Micropterus punctulatus</i>	Centrarchidae	3*		104*								
Spotted Sucker	<i>Minytrema melanops</i>	Catostomidae			7*								
Stippled Darter	<i>Etheostoma punctulatum</i>	Percidae			115								
Stonecat	<i>Noturus flavus</i>	Ictaluridae	88	15	21	35	13	16	8	32			
Striped Bass	<i>Morone saxatilis</i>	Moronidae		2*							1*	2*	
Striped Shiner	<i>Luxilus chrysocephalus</i>	Cyprinidae			109								
Sturgeon Chub	<i>Macrhybopsis gelida</i>	Cyprinidae								2			

Common name	Scientific name	Family	Missouri River biogeographic region								Colorado River biogeographic region		
			CN	KS	LM	PN	SJ	UM	WL	YS	LC	MC	UC
Suckermouth Minnow	Phenacobius mirabilis	Cyprinidae	242	41	135	22	1						
Tadpole Madtom	Noturus gyrinus	Ictaluridae	17		10		1		1*				
Threadfin Shad	Dorosoma petenense	Clupeidae									2*		
Topeka Shiner	Notropis topeka	Cyprinidae	7	14	17								
Trout-perch	Percopsis omiscomaycus	Percopsidae	12										
Utah Chub	Gila atraria	Cyprinidae											4*
Utah Sucker	Catostomus ardens	Catostomidae											1*
Virgin River Chub	Gila seminuda	Cyprinidae										1	
Virgin Spinedace	Lepidomeda mollispinis	Cyprinidae										19	
Walleye	Sander vitreus	Percidae	6*			2*	1*	8*	3*	2*		1*	
Warm Springs Pupfish	Cyprinodon nevadensis pectoralis	Cyprinodontidae										2*	
Warmouth	Lepomis gulosus	Centrarchidae			38								
Wedgespot Shiner	Notropis greenei	Cyprinidae			17								
Western Blacknose Dace	Rhinichthys obtusus	Cyprinidae	28*				2*						
Western Mosquitofish	Gambusia affinis	Poeciliidae	29*	12*	216*	29*					73*	5*	2*
Western Silvery Minnow	Hybognathus argyritis	Cyprinidae	2					35	2	71			
White Bass	Morone chrysops	Centrarchidae	4	2*	6		2*						1*
White Crappie	Pomoxis annularis	Centrarchidae	56	15	75	7	1	2*	1*	1*			
White Perch	Morone americana	Moronidae				2*							
White River Spinedace	Lepidomeda albivallis	Cyprinidae										1	
White River Springfish	Crenichthys baileyi	Goodeidae										4	
White Sucker	Catostomus commersonii	Catostomidae	234	45	268	136	17	244	45	192			207*
Woundfin	Plagopterus argentissimus	Cyprinidae										2	
Yaqui Chub	Gila purpurea	Cyprinidae									3*		
Yellow Bass	Morone mississippiensis	Moronidae	1*										
Yellow Bullhead	Ameiurus natalis	Ictaluridae	190	47	284	27		2*	1*	7*	41*	2*	
Yellow Perch	Perca flavescens	Percidae	6*					23*	4*	14*			5*

CHAPTER 5- MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

Summary

In this study, I used landscape-level environmental data and fish sampling records to explain patterns in fish distributions and inform lotic fish conservation efforts. First, I developed an approach to identify potentially ecologically important tributaries (PEITs) using watershed characteristics and evaluated the effects of these tributaries on small-bodied fish assemblage (Chapter 2). Using this approach, I identified one PEIT for the middle Missouri River, three for the San Juan River, and four each for the lower Missouri, upper Colorado, and lower Green Rivers that may be targeted for conservation efforts because they are likely to affect flow, sediment, or temperature regimes of these mainstem rivers, assuming these factors are driven by watershed area, surficial lithology, and dam storage density. This approach also provides management agencies with information that may be used to prioritize tributaries for restoration and protection. For example, the Osage River may be targeted for restoration because it increased mainstem Missouri River hydrological alteration (measured by dam storage density), whereas the Niobrara and Platte Rivers could be prioritized for protection because they reduced mainstem hydrological alteration. Finally, this approach for identifying PEIT can be used to delineate ecologically relevant sampling reaches and may identify tributaries that have distinct chemical signatures for microchemistry studies; both of these applications are likely to improve our understanding of large river ecology and, subsequently, conservation efforts.

My research on spatial transferability of species distribution models (SDMs; Chapter 3) and the drivers of non-native species establishment (Chapter 4) provided insights into the factors associated with non-native species occurrences that can inform management actions, but also suggested that caution should be used when implementing management actions based on predicted distributions of non-native species. First, SDMs transferred spatially for 60% of the species that I evaluated, suggesting that SDMs may be used in some cases (e.g., when important predictor variables and species-variable relationships are consistent between regions) to predict areas of non-native species establishment. However, transferability was not predictable by species characteristics and may be species- and context-specific, so it is unclear when it would be appropriate to implement management decisions based on spatially-transferred SDMs. Second, these studies suggested natural environmental factors may be the most important factors driving non-native species at the stream segment spatial grain because natural factors were often identified as the most important variables in SDMs (Chapter 3), and metrics of human activity and the native fish assemblage rarely resulted in models that explained substantial variability in the probability of non-native family occurrence (Chapter 4). Third, I found that support for the hypothesized drivers of non-native family occurrence varied by spatial extents and families, suggesting that results from studies at coarse taxonomic scales and across large spatial extents may not be reliably generalized to other taxonomic groups or spatial extents. Therefore, results from large-scale studies may not adequately explain the drivers of non-native species at smaller scales that are more applicable to resource managers. Finally, although I found little evidence of differences in SDM transferability related to species characteristics, it is concerning that the species

characteristics that were hypothesized to result in high SDM transferability (e.g., highly specialized traits) are opposite those of species that were expected to be successful invaders (e.g., generalist species). Therefore, using SDMs to predict future distributions of non-native species could have limited utility if the hypothesized relationships between species characteristics, SDM transferability, and invasion success are correct.

In conclusion, understanding how landscape-scale environmental factors structure lotic ecosystems can improve conservation efforts, but care should be taken to ensure that appropriate spatial and taxonomic scales are considered. In this study, I found that the effects of PEIT on fish assemblage structure and the drivers of non-native species varied among rivers (Chapter 2) and spatial extents (Chapters 3 and 4). These results highlight the need to focus research efforts on spatial and taxonomic scales relevant to resource managers. Although large-scale (e.g., global spatial extent and species richness) analyses may identify interesting ecological patterns, studies at these scales may have limited value to decision-makers that manage individual species or watersheds. Furthermore, these large-scale studies may provide correlative relationships, but may not identify mechanistic linkages that are needed to provide confidence that management actions will be effective.

Future Research

Our understanding of the value of tributaries to large river conservation could be improved by research that identifies the mechanisms responsible for tributary effects on abiotic and biotic components of large river ecosystems. My results showed that PEIT may affect small-bodied fish assemblage structure, but my ability to evaluate potential mechanisms responsible for the effects of PEIT was limited by insufficient data adjacent

to numerous PEIT, the fact that PEIT were often identified by multiple landscape factors, and the limited availability of abiotic and biotic response data. In this study, I limited analysis to small-bodied fish assemblage structure because fish sampling data was readily available for large rivers from the Pallid Sturgeon Population Assessment Program and the Upper Colorado River Endangered Fish Recovery Program, whereas large-scale data was limited for abiotic factors and lower trophic levels (e.g., invertebrates). Future research could improve our understanding of the mechanisms responsible for tributary effects by focusing research efforts on tributaries identified by only one landscape factor to reduce potential confounding of multiple mechanisms operating simultaneously. Furthermore, future studies could provide a more complete understanding of tributaries by studying their effects on abiotic and biotic metrics directly related to tributary inputs. For example, a potential study design would be to evaluate the effects of tributaries identified by surficial lithology on substrate composition, turbidity, and, subsequently, the abundance and diversity of fish and invertebrates using a traits-based approach (e.g., substrate and turbidity preferences).

Our understanding of the drivers of non-native fish establishment in lotic ecosystems could be improved by 1) resolving issues related to spatial scale, 2) incorporating natural abiotic factors, biotic factors, and metrics of human activity as predictor variables when evaluating the drivers of non-native species, and 3) synthesizing the results of non-native SDMs across species. First, I found it challenging to synthesize the results of previous studies that evaluated the hypothesized drivers of species invasions because spatial grain and spatial scales were not always clearly identified and often varied among studies. In addition to improved consistency and clarity in spatial scale

reporting, I suggest that examining species invasions as a stepwise habitat filtering process (Tonn 1990; Poff 1997; Jackson et al. 2001) may provide valuable insight on the effects of spatial scale on the drivers of species invasions. Second, I did not include natural abiotic factors as potential predictors of non-native family occurrence (Chapter 4) because previous studies supported the hypothesized drivers without inclusion of natural factors in their analyses, but these models generally explained little variability (pseudo- $R^2 < 0.2$) in non-native family occurrence in this study. Meanwhile, I did not include biotic metrics as predictor variables in SDMs because fish sampling data is likely unavailable for most areas of potential non-native species introduction, so including these variables would not accurately represent SDMs used to predict non-native species invasions. However, including the suite of biotic, natural, and anthropogenic factors into these analyses (e.g., Chapters 3 and 4) could help identify whether human activity and native fish assemblage structure are the primary drivers of non-native species occurrence, or if these factors are of secondary importance to natural factors. Finally, comparing non-native SDMs that incorporate natural factors, human activity, and the native fish assemblage metrics as predictor variables among multiple species could help identify patterns in the drivers of non-native species. Studies that evaluate the drivers of non-native species establishment at the species taxonomic scale are likely more informative than studies at generalized biotic scales (e.g., non-native species richness) because they do not assume that the drivers of establishment are similar among species that may have different traits and ecology (Lapointe and Light 2012). It is unlikely that this assumption is met in all situations because my research showed that the primary abiotic drivers of species distributions varied among basins for most species (Chapter 3) and the drivers of

non-native family occurrence differed among families and spatial extents (Chapter 4). By evaluating the drivers of individual species distributions first, then comparing these results across species, one could evaluate which hypotheses (i.e., Biotic Resistance, Biotic Acceptance, and Human Activity) are most-supported even if the specific variables driving distributions differ among species. This type of study would fill a gap in the invasive species literature because most studies at the species taxonomic scale focus on a limited number of species, and studies that model distributions of numerous species rarely synthesize their results in the context of the drivers of non-native species (e.g., Chapter 3).

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VITA

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