Enhancing conservation of large-river biodiversity by accounting for tributaries

Brenda M Pracheil[1*], Peter B McIntyre[1], and John D Lyons[2]

Alteration of rivers for human use has resulted in substantial biodiversity declines, particularly for species restricted to the largest rivers. Conservation and restoration efforts on large rivers often focus on the mainstem, but societal reliance on benefits derived from these alterations generally prevents complete restoration of the river. We propose that certain tributaries, by virtue of their lower degree of alteration, offer underappreciated opportunities for conserving large-river biota. Using the distribution patterns of large-river specialist fishes from the Mississippi River Basin, we identify a threshold discharge (166 cubic meters per second) beyond which tributaries support all or most of these species. We merge our macroecological analysis of assemblage structure with data on dam locations to identify tributaries where restoration efforts offer the highest potential conservation gains for 60 of the 68 large-river specialist fish species that are of state, federal, or international conservation concern. Given the highly altered state of many mainstem rivers, this analytical approach could be used to select tributaries that will aid in the conservation of large-river species worldwide.

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Massive engineering projects and habitat degradation on the world's largest rivers have led to severe biodiversity losses (Dudgeon *et al.* 2006; Vörösmarty *et al.* 2010). Species with life histories that are particularly suited to the high discharge, habitat heterogeneity, and long-distance migratory corridors of large rivers have experienced especially marked declines. For example, fishes of the Order Acipenseriformes (paddlefish and sturgeon) were recently named the most endangered taxon on Earth by the International Union for Conservation of Nature (IUCN), in part resulting from degradation of the large-river habitats used by most of these species (Lenhardt *et al.* 2006).

Realistically, our ability to reduce or offset human impacts on large-river biodiversity is limited despite the hundreds of millions of dollars spent on these conservation efforts in the US alone (Bernhardt *et al.* 2005). Large rivers are integral components of transportation, power production, and water supply infrastructure, but the same engineering projects that facilitate human uses also play a central role in the decline of biodiversity. Continued societal reliance on the benefits of such river alterations frequently makes their removal an untenable conservation strategy. Moreover, the vast spatial extent of large-river watersheds complicates management interventions, particularly those aimed at diffuse stressors – such as pollution, invasive species, and fish harvest – that are typically mitigated through small-scale (eg state and local government) approaches. Consensus and coordination of appropriately large conservation plans are further complicated by the need to represent multiple political jurisdictions and diverse stakeholder interests. This complex suite of factors makes conservation and restoration of large rivers themselves difficult, thus further limiting recovery options for already imperiled species dependent on these ecosystems.

Here, we posit that large tributaries offer underappreciated opportunities to conserve large-river specialist species by serving as high-value mainstem restoration surrogates or supplements that can restore some ecosystem function in spite of mainstem river alterations. Previous studies have suggested that tributaries may be useful biodiversity conservation targets when societal reliance on mainstem alterations prevents restoration (Pracheil *et al.* 2009). For instance, relatively unaltered tributaries can sometimes fulfill habitat and life-history requirements for large-river specialist fishes after the mainstem has been altered by dams or other development projects (Neely *et al.* 2009; Pracheil *et al.* 2009; Ziv *et al.* 2012). Furthermore, because of smaller watershed size, integrating tributaries into large-river conservation plans may have practical benefits by decreasing the number of jurisdictions and stakeholders involved in implementing a given project. However, quantitative methods for identifying the most suitable tributaries have not been established.

Using the Mississippi River Basin of the central US as a case study, we assess which tributaries are most promising as conservation targets for large-river species by evaluating biogeographic patterns and dam locations. Olden *et al.* (2010) have suggested the importance of advancing trait-based biogeography of freshwater fishes for informing conservation planning. In this spirit, we use a biodiversity analysis rooted in the positive macroecological relationship between species richness and river discharge (Oberdorff *et al.* 2011) to identify tributaries of high con-

[1]*Center for Limnology, University of Wisconsin, Madison, WI* [*]*(pracheil@wisc.edu);* [2]*Wisconsin Department of Natural Resources, Madison, WI*

servation value to large-river specialist fishes. We focus specifically on large-river specialist fishes – the distributions of which are limited to large rivers – and assess whether there is a minimum river discharge for these species to utilize a particular tributary. We also examine the role of discharge on large-river specialist assemblage structure to improve our understanding of the potential gains of using tributaries as restoration targets. We then apply the empirical discharge threshold to all Mississippi Basin tributaries, to allow identification of the tributaries most capable of supporting diverse assemblages of large-river specialist fishes. By altering hydrology, blocking migrations, and fragmenting populations, dams are a major threat to large-river specialist fishes (Reidy Liermann *et al.* 2012); we therefore compare the length of tributary where the connection to the mainstem is unobstructed as a metric of conservation gains.

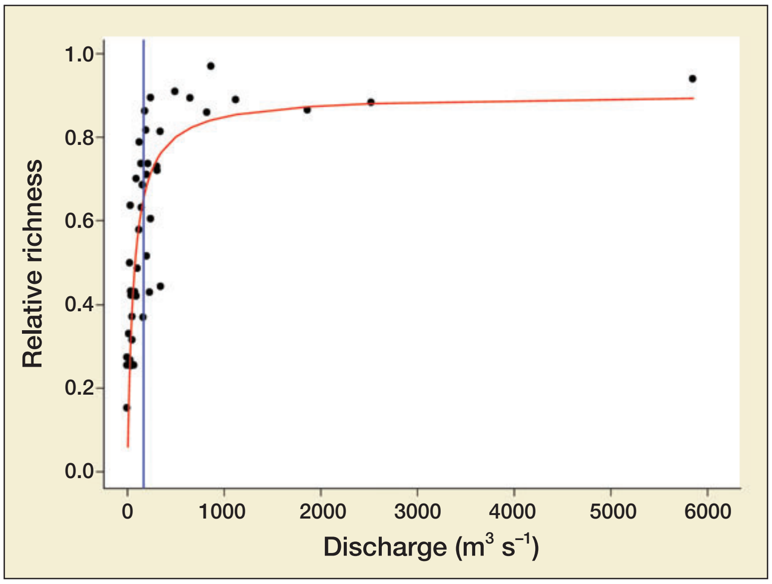

Figure 1. *Relative richness of large-river specialist fishes from 43 Mississippi River Basin tributaries, including relative richness of the Missouri, Arkansas, and Ohio rivers using the Mississippi River to define the mainstem species pool. The best-fit line from a Michalis–Menten function (red curve) and the discharge threshold determined by split linear regression analysis (166 m^3 s^{-1}; blue line) are indicated.*

Methods

Our study focuses on the Mississippi River Basin because its fish species distributions and tributary discharges are well-known, as compared with those of most of the world's large rivers. To account for differences in species pools and overall richness, we examined biodiversity relationships to tributary discharge in the four largest sub-basins (basin area > 250 000 km^2): the Arkansas, the Mississippi, the Missouri, and the Ohio. Where a sub-basin was named after a river, that river was considered the mainstem. We further subdivided the mainstems into a total of seven regions (WebTable 1) based on longitudinal shifts in their faunas, so that each area had a characteristic pool of large-river specialist species.

Because discharge is a strong predictor of riverine biodiversity patterns (Muneepeerakul *et al.* 2008; Hugueny *et al.* 2010; Oberdorff *et al.* 2011), we analyzed relationships between discharge and patterns of large-river specialist species richness and assemblage structure. For each of 43 tributaries, we quantified relative richness of large-river specialist fishes, which we defined as the proportion of these species from the regional mainstem that were also present in a tributary (WebTable 2). Presence/absence information used in relative richness calculations was based on published species lists and local expert input (WebPanel 1).

We analyzed the relationship between relative richness and mean annual discharge across all tributaries. To account for apparent non-linearity, we used a split linear regression break-point analysis to identify a river discharge threshold in relative richness (WebPanel 1). We also examined the influence of discharge on assemblage structure of large-river specialists. We quantified nestedness of species across all tributaries in each region using nestedness temperature (T, where $T = 0$ and $T = 100$ represent fully nested and fully random assemblages, respectively; WebPanel 1). To test whether discharge is an organizing factor in assemblage structure, we used Spearman's rank correlations to compare discharge and tributary rank-order from the nestedness analysis species-packing matrix within each region. A weighted z test was used to test significance of the relationship across all regions (WebPanel 1).

To delineate potential tributary conservation targets for large-river specialists, we identified all tributaries in the Mississippi River Basin above the discharge threshold using a geographic information system (GIS; WebPanel 1). For this subset of tributaries, we quantified tributary length where (1) dams did not interrupt fish movement between mainstem and tributary and (2) discharge met or exceeded the threshold (WebPanel 1). Tributary reaches where fish movement was unobstructed by dams and where discharge exceeded the threshold were considered the best potential targets for conservation efforts.

Results

There was a clear discharge threshold above which tributaries contained ≥ 80% of the local pool of large-river specialists (Figure 1). Split linear regression identified the threshold discharge as 166 ± 26 m^3 s^{-1} (mean ± standard error; adjusted $r^2 = 0.64$; Figure 2). The largest tributaries are utilized by virtually every species in the four mainstems examined (Figure 2; WebFigure 1). For example, the Platte and Kansas rivers together contain all large-river specialist species in the Middle Missouri region (WebFigure 1), and the Wisconsin River contains 23 of

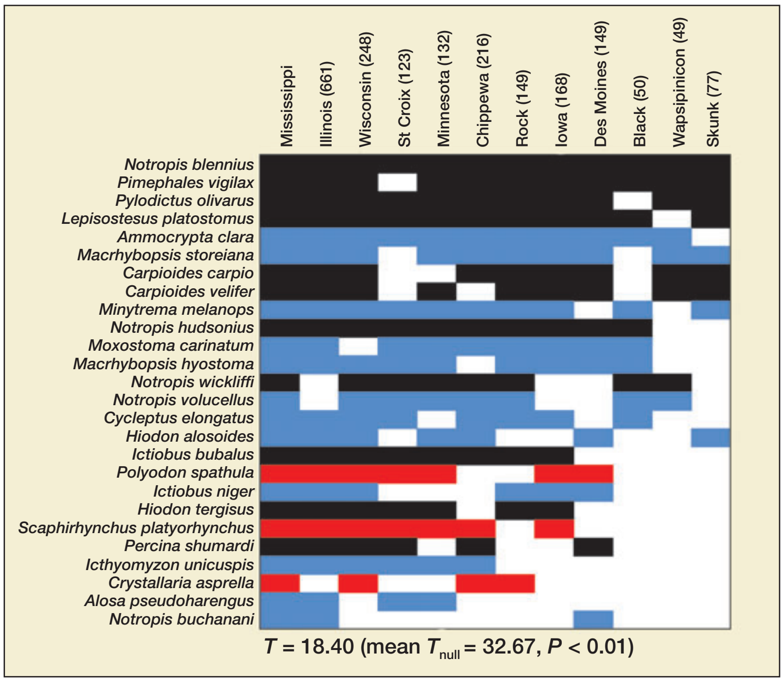

Figure 2. *Species packing matrix for Upper Mississippi region and its tributaries, illustrating large-river specialist species present and of no official conservation concern (black bars); listed as state vulnerable, threatened, or endangered (blue bars); or listed on the IUCN Red List (red bars). Mean annual discharge (m^3 s^{-1}) for each tributary is in parentheses. Nestedness temperature (*T*) for this matrix and mean temperature of 2000 random matrices (mean T_{null}), where* T *= 0 represents a perfectly nested community and* T *= 100 represents a totally random community, are shown below the figure. The* P *value is the probability that the large-river specialist assemblage could occur at random.*

26 large-river specialists within the Upper Mississippi region (Figure 2).

Large-river specialist fishes are highly imperiled; 60 of the 68 species in our analyses are of special concern for conservation at state, federal, or international levels (Figure 2; WebFigure 1). Assemblages of all large-river specialist fishes were highly nested across tributaries, showing significant deviations from random patterns (Figure 2; WebFigure 1). Values for *T*, which quantify the strength of assemblage nesting, ranged from very high (7.61) in the Middle Mississippi region (WebFigure 1) to moderately high (18.40) in the Upper Mississippi region (Figure 2). Across all regions, assemblage structure of large-river specialist fishes is closely associated with discharge (weighted *z* test, $P < 0.001$; WebFigure 2); most species are more likely to be found in large tributaries than small ones, but individual species differ in the minimum discharge at which they are reported. These strong patterns suggest that tributary size is a general predictor of how many and which species may benefit from restoration. For full details of species lists and nestedness patterns for all 43 tributaries in the relative-richness discharge analysis, see WebFigure 1 and WebTable 2.

We identified many tributaries in the Mississippi Basin that lack dams and have mean annual discharge exceeding the threshold, suggesting they are promising conservation targets for large-river specialist fishes. Some of these tributaries include long, unobstructed stretches connected with the mainstem (WebTable 3; Figure 3). For instance, 11 tributaries contain >100 km of unobstructed length where discharge exceeds the threshold (WebTable 3). Of particular note are the Yellowstone, Des Moines, Yazoo, White (Ohio), and Wabash rivers, as well as the White-Black river system, each of which offer >200 km of unobstructed length above the discharge threshold (WebTable 3).

Discussion

This study provides a simple, biologically rooted framework for guiding large-river conservation planning by identifying tributaries large enough to serve as natural surrogates for mainstem ecosystems. Our approach was inspired by the fact that many large-river specialist fishes are known to use large tributaries as well as mainstems (Neely *et al.* 2009; Pracheil *et al.* 2009; Ziv *et al.* 2012); discharge itself might therefore indicate which tributaries could provide the greatest conservation value for these species. We show that tributary discharge has a strong influence on species richness and assemblage structure among large-river specialists, reflecting the habitat requirements of individual species. Thus, tributary discharge can be an informative initial criterion for assessing which tributaries offer the most promise for conservation efforts in the absence of detailed population and habitat information.

The sharp threshold in tributary discharge together with the relative richness of large-river fishes suggests that tributaries below a certain size have far less potential for benefiting large-river specialists than larger tributaries. Tributaries larger than the discharge threshold have fairly comparable mainstem faunal composition and assemblage structure, thereby allowing for prioritization of conservation efforts among these large tributaries to be based on other factors, such as dam location (as in this study), or other tributary attributes that can benefit biota, such as geomorphic or hydrologic factors that no longer exist on the mainstem. For example, the unimpounded lower reaches of the Wisconsin River provide 92 additional river kilometers from the lowest dam on the Wisconsin River to Mississippi River Lock and Dam 10 (the next downstream dam) than the adjacent reach on the mainstem Mississippi River (from Lock and Dam 9 to 10). Increases in longitudinal distance may be critical for large-river specialist species, such as shovelnose and pallid sturgeon (*Scaphirhynchus platorynchus* and *Scaphirhynchus albus*, respectively), which require long larval

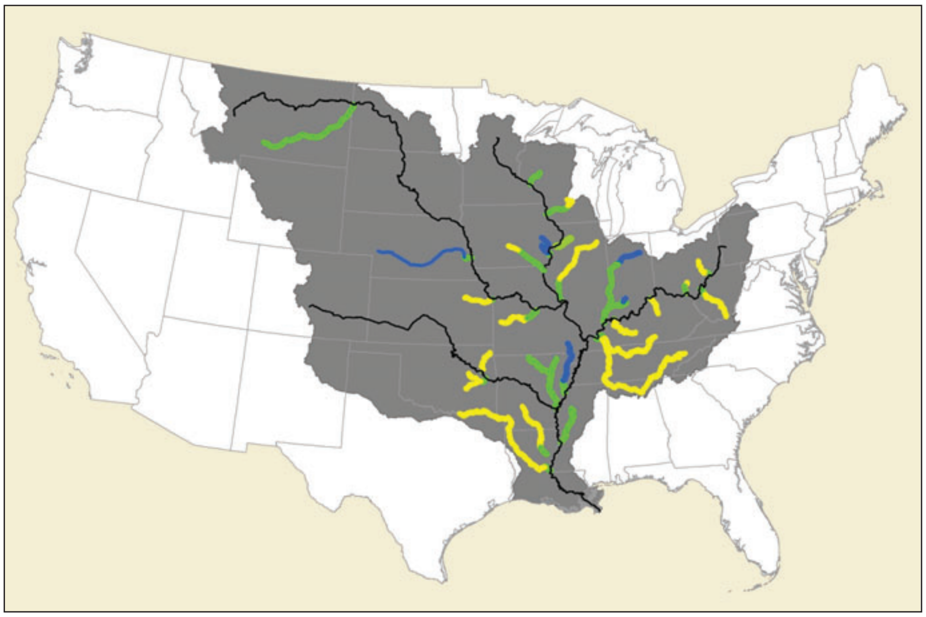

Figure 3. *Mississippi River Basin (gray polygon), large-river mainstems (black lines), and tributary reaches exceeding, equal to, or below the threshold discharge (166 m^3 s^{-1}) at confluence: unobstructed longitudinal connectivity from confluence where discharge ≥ threshold (green lines); upstream of a dam but discharge ≥ threshold (yellow lines); and unobstructed longitudinal connectivity from confluence where discharge < threshold (blue lines).*

drift distances for survival (Braaten *et al.* 2008). Furthermore, greater hydrologic variability of tributaries provides essential spawning cues that are now absent in mainstems with homogenized hydrology (Poff *et al.* 2007) for large-river specialist fishes, such as paddlefish (*Polyodon spathula*; Pracheil *et al.* 2009) and blue sucker (*Cycleptus elongatus*; Neely *et al.* 2009).

Protecting large-river specialist biodiversity presents special challenges because the habitat needs of these species limit their distribution to the same rivers where humans have developed major infrastructure projects. As a result, conserving these species in mainstem rivers often requires costly interventions. Our findings indicate that conservation investments in select tributaries may economically complement mainstem efforts. We are not suggesting that tributaries offer a one-to-one replacement for degraded mainstem habitats. Historically, mainstems had high discharges, longitudinal distances, hydrological variability, and habitat complexity that is unmatched by tributaries, and current conditions in tributaries often differ tremendously from current and historical mainstem conditions (Sabo *et al.* 2012). However, given the constraints on mainstem restoration and the ability of tributaries to help support imperiled species despite these constraints, the analytical approach we used provides practitioners with a means to identify additional high-value restoration targets that may be politically and economically feasible.

Our results offer a model for how biogeographic thresholds in environmental conditions can combine with measures of habitat degradation to guide conservation efforts, but we caution that this framework should be used alongside other approaches. Even at the scale of the Mississippi River Basin, the results show that excluding tributaries that fall slightly under the discharge threshold may exclude areas of known importance to large-river specialist species. For example, the Minnesota River contains 73% of large-river specialists found in the Upper Mississippi region, but its mean annual discharge is 79% of the discharge threshold (WebTable 1). Our analyses also assume that the discharge threshold evident across tributaries is applicable within each individual tributary, so that large-river specialists will use only the lower reaches where discharge exceeds the threshold. Relaxing this assumption could change which portions of tributaries are highlighted as having the greatest conservation potential. Finally, we focused on large-river specialist fishes because they represent a special conservation challenge, but more widespread species may not exhibit similar discharge-associated distributional limits. As a result, our approach should not be broadly applied for conservation of riverine biodiversity in general.

We suggest that conservation actions in tributaries could benefit large-river specialist species for which current policy and management focus primarily on mainstem habitats. For example, ecosystem recovery plans for the Platte (a tributary of the Missouri River) and Missouri rivers involve quotas for specific habitats (eg shallow water habitat, sandbar habitat). Although large-river specialist fishes use these rivers somewhat interchangeably (Neely *et al.* 2009) and the Platte River contains 577 km of unimpounded, relatively unaltered habitat (as compared to the highly altered mainstem), administrative guidelines mandate that tributary restoration actions cannot count toward mainstem quotas despite many shared conservation benefits. While it would be irresponsible to allow tributary conservation efforts to replace mainstem conservation projects, recognizing the ecological benefits that tributary restoration efforts provide to mainstems would be sensible in large-river ecosystem recovery plans.

Joint spatial analysis of tributary size and dam placement can also aid conservation and restoration efforts targeted at large-river specialist species. Explicit consideration of tributary dams is critical when creating large-river conservation plans. Recent evaluations of planned dams in the Mekong (Ziv *et al.* 2012) and Amazon (Finer and Jenkins 2012) basins suggest that impounding certain tributaries will have disastrous consequences for biodiversity and ecosystem services, while others are of less concern. In the US, new dam construction has all but ceased, but many (ie non-congressionally authorized) are relicensed every 30–50 years by the Federal Energy Regulatory Commission (FERC). The FERC relicensing process includes a biological impacts assessment that can ultimately require restorative actions as a condition of license reissue. For example, after the extirpation of several large-river specialist fishes, the FERC relicensing agreement for the lowest dam on the Wisconsin River mandated fish passageway construction to reconnect a reach above the dam with the Mississippi River (Lyons 2005). Even when historical data on species distributions are unavailable to assess specific dam impacts, relationships between large-river specialist species and tributary discharge like those documented in this study can provide some perspective on the ecological consequences of decisions. Our approach could also be useful for large-river specialist fish conservation in areas of the globe where major interbasin water-transfer projects are being planned or are underway (Grant *et al.* 2012), particularly in cases where more detailed data are not available.

In the decade since Abell (2002) highlighted the biodiversity crisis in freshwater ecosystems, few advances have been made to protect the largest rivers. During this same 10-year period, enormous new infrastructure projects have been initiated along many of the world's great rivers, including biodiversity hotspots such as the Mekong (Ziv *et al.* 2012) and Amazon (Finer and Jenkins 2012) rivers. Infrastructure planning is outpacing conservation planning along these large rivers, creating a pressing need to devise politically and economically feasible approaches for protecting their biodiversity. Even in wealthy nations where governments seek to avoid species loss, societal dependence on large-river ecosystem alterations reduces the likelihood of fundamental restoration of most mainstems. Here, we have presented a framework that can help identify tributaries large enough to help support specialized fauna of mainstem rivers, particularly where dams or other forms of habitat degradation are absent. As human use of large rivers expands, such approaches will become increasingly important for conserving their specialized biota.

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