

Implications of Dam Obstruction for Global Freshwater Fish Diversity

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*Dams are obstructing rivers worldwide, impairing habitat and migration opportunities for many freshwater fish species; however, global data linking dam and fish distributions have been limited. Here, we quantify dam obstruction at the biogeographic scale of freshwater ecoregion, which provides the spatial framework necessary to assess the risk of fish species loss due to dams and allows us to identify both ecoregions and genera at risk. Nearly 50% of the 397 assessed freshwater ecoregions are obstructed by large- and medium-size dams, and approximately 27% face additional downstream obstruction. A synthesis of obstruction data and fish traits indicates that taxa such as lampreys (*Lampetra* spp.), eels (*Anguilla* spp.), and shads (*Alosa* spp.) are at particular risk of species loss. Threatened ecoregions with heavy dam obstruction and above-average counts of total, diadromous, or endemic species are found on all continents and include the Murray–Darling Province, Southern Italy, the Lower and Middle Indus Basin, West Korea, the South Atlantic region of the United States, the Upper Paraná, and Mobile Bay ecoregions.*

Keywords: dams, ecoregions, fish, rivers

The world's freshwaters are underinventoried (Stiassny 2002), lose species faster than terrestrial or marine biota (Sala et al. 2000), and face mounting anthropogenic impacts (Dudgeon et al. 2006, Arthington et al. 2010). Dams constitute a major threat to global freshwater species diversity (Vörösmarty et al. 2010); they lead to loss of native species but also to invasion by exotic species, partly because exotic species are likely to establish in modified or degraded freshwaters (Poff et al. 2007). The implications of dam obstruction for local freshwater diversity have been examined in small-scale studies (e.g., Anderson et al. 2006), but a paucity of regional- or global-scale information has constrained large-scale freshwater management planning (but see Thieme et al. 2007). Dams remove turbulent river sections and create tranquil water bodies, thus affecting, for example, flow and temperature regimes, sediment transport, and species communities. The shift from lotic to lentic environments after dam construction often favors generalist over specialist species, and it alters assemblages of taxonomic groups and puts endemic species at particular risk of extinction, which leads to biotic homogenization (Rahel 2000, Poff et al. 2007). Shifts in temperature regime, including downstream decreases in temperature that result from hypolimnic releases from reservoirs, impair conditions favorable to native species but may favor exotics or

habitat generalists (Roberts 2001). Dams retain sediment, which limits the downstream substrate available for critical life-stage habitats such as nesting and refuge for many species (Černý et al. 2003). Reductions in sediment transport also affect receiving seas, with implications for diadromous, estuarine, and marine species (Baisre and Arboleya 2006). In fact, many river deltas are sinking because of compaction and reduced sediment delivery, which increases their vulnerability to natural disturbances (Day et al. 2007).

Dams inhibit organism migration, alter and fragment habitats, and reduce resource transport throughout rivers (Roberts 2001, Hall et al. 2011), thus affecting species distributions among aquatic trophic levels and terrestrial ecosystems (Nilsson et al. 1997, Pringle et al. 2000). Fish are the most important example. Dams obstruct the migration of fish to spawning or feeding grounds or impede the function of these grounds by changing water depths, currents, and deposition patterns, leading to senescence prior to reproduction (Kruk and Penczak 2003, McLaughlin et al. 2006). Migration through hydropower dam turbines also causes mortality, especially of adult fish (Larinier 2000). For resident or potamodromous fish, competition for spawning sites and food can increase as dams disconnect, isolate, and reduce the number and size of habitats (Cambray et al. 1997). Genetic pools of resident populations may also decrease with the

isolation created by dams (Nielsen et al. 1997). Sometimes, this isolation may prove beneficial for native biota by blocking the entry of invasive species (McLaughlin et al. 2007) or of pollutants, parasites, or diseases into the habitat. The important implications of dam obstruction for freshwater species richness are highlighted by the myriad ways in which species loss affects trophic groups and ecosystem functioning (Cardinale et al. 2006). For example, Pacific salmon (*Oncorhynchus* spp.) contribute ocean-derived nutrients in addition to catchment inputs, thereby increasing primary and secondary production (Helfield and Naiman 2006). Many of the effects of dams may be intertwined with or result entirely from non-dam-related land-use changes (Malmqvist and Rundle 2002). However, dams are the factor most consistently documented (Lehner et al. 2011), are considered one of the greatest threats to freshwater biodiversity worldwide (Vörösmarty et al. 2010), and can serve as an indicator of other human activities (Nilsson et al. 2005). Until now, a lack of data depicting freshwater fish distributions precluded a global assessment of dam-related threats to freshwater species (see Nilsson et al. 2005).

In this article, we map dam obstruction at a scale useful for global planning of freshwater research and management. Specifically, we identify regions and freshwater fish taxa along a gradient of risk for species loss due to dam obstruction and its associated ecohydrologic impacts (hereafter referred to summarily as *dam obstruction*). We achieved this by quantifying and mapping obstruction by dams in the world's freshwater ecoregions and then integrating these results with ecoregional fish-distribution data. For each ecoregion, we used obligate diadromous behavior and endemism as indicators of potential species loss due to dam obstruction. Obligate migratory behavior in fishes is a lead trait contributing to their vulnerability to dam obstruction, which has led to the documented extirpation and imperilment of many species (Penczak et al. 1998). Because endemic species are restricted in the extent of their habitat, they are inherently more at risk of loss than are non-endemics when faced with potential habitat alteration (Scott and Helfman 2001, Brooks et al. 2002) such as that posed by dams. Whereas a widespread native species may not be threatened globally by the myriad impacts of dams, an endemic species could be extirpated. We included an assessment of where freshwater habitat alteration may compound the effects of dam obstruction and identified ecoregions faced with additional external downstream dam obstruction. Of the numerous additional threats that we could possibly include in our analysis, habitat alteration is one for which the effects on freshwater fishes are well documented (e.g., Light and Marchetti 2007, Leprieur et al. 2008), and the inclusion of this variable addresses the difference between dam impacts in an otherwise undisturbed landscape and those in a heavily disturbed one. Finally, we compared the distribution of the ecoregions most heavily obstructed by dams with the distribution of catchments in which fish are endangered by projected changes in climate and water

withdrawal (Xenopoulos et al. 2005), highlighting parts of the world that may be at the greatest risk of freshwater species losses due to cumulative threats.

Study area

We included 397 freshwater ecoregions of the world in our analyses and used available georeferenced dam and fish-distribution data (figure 1; also see supplemental appendix S1, available online at <http://dx.doi.org/10.1525/bio.2012.62.6.5>). Freshwater ecoregions represent environmental and ecological variables known to influence species distribution. They are defined here as large areas of freshwater that contain a geographically distinct assemblage of natural communities that share a large majority of their species and ecological dynamics, that share similar environmental conditions, and that interact ecologically in ways that are critical for their long-term persistence (Abell et al. 2008). Over 130 ichthyologists and freshwater biogeographers analyzed data on species distributions, phylogenetic history, palaeogeography, and ecology to delineate the world's freshwater ecoregions. The resulting units may align with basin boundaries but may also encompass multiple basins or portions of basins. For example, the Amazonas High Andes ecoregion in South America encompasses just the uppermost portions of the headwaters of numerous Amazonian tributaries, the São Francisco ecoregion aligns perfectly with the São Francisco basin, and the Mata Atlántica ecoregion comprises over 20 coastal basins.

Mapping dam obstruction

An ecoregion without georeferenced dams but for which indications of dams were found in the literature was reported to have insufficient data for analysis. Dams at the boundary of an ecoregion were not considered to obstruct the fish within the ecoregion; the rarity of these cases is not thought to exert bias. River channels drawn on the map (Groves et al. 2002) were derived from multiple fine-resolution sources to provide a more realistic depiction of hydrography than digitally available data could (e.g., the available digital hydrographies were modeled at insufficient resolutions). However, it was necessary to measure unobstructed water-courses using digital hydrographies for a limited number of cases in which a dam that was accurately depicted digitally could not be located on the printed map. A comparison of the two methods for areas of shared data availability showed a negligible difference and no consistent bias in the results. The digital data on dams (USEPA 1998, Vörösmarty et al. 2003, Lehner and Döll 2004, Nilsson et al. 2005, FAO 2006, with additions from the University of Yamanashi in Japan, the National Institute of Water and Atmospheric Research in New Zealand, World Wildlife Fund Canada, and Greifswald University in Germany) were synthesized in ArcGIS 9.0 (ESRI, Redlands, California), and exclude millions of small dams and weirs (that are less than 15 meters high) that are estimated to exist worldwide but for which georeferenced data do not exist (e.g., several million small dams are

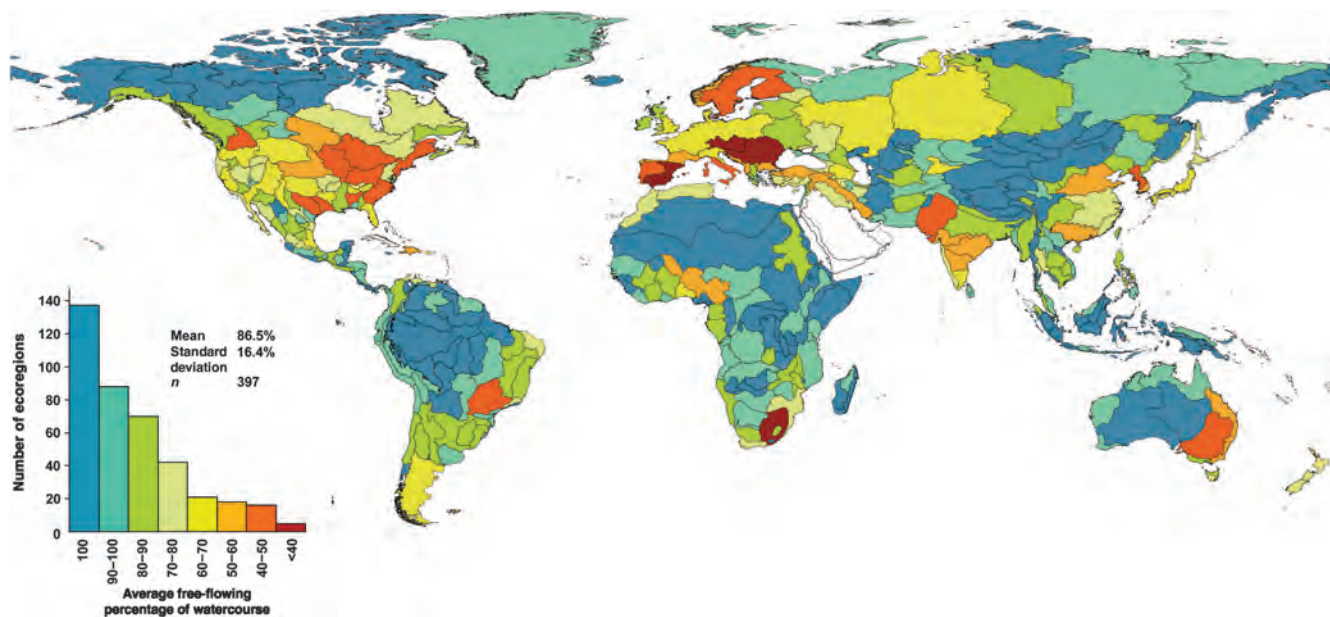


Figure 1. Distribution of the average free-flowing percentage of watercourse length among the 397 freshwater ecoregions with available data. The data are skewed; the five longest watercourses of approximately half of all of the ecoregions ($n = 215$) retained an average of 90%–100% of their watercourse distance as free flowing. The white areas indicate a lack of sufficient data for analysis. No dams were identified on the five longest watercourses of 137 ecoregions (indicated by the darkest blue).

estimated for the United States alone; Renwick et al. 2005). This exclusion implies that average dam obstruction for an ecoregion is likely greater than the reported amount and that the impacts are underestimated.

For each ecoregion, dam obstruction was quantified in two steps. First, we measured the longest undammed distance of each of an ecoregion's five longest connected freshwater pathways, regardless of stream order and including lakes, and recorded these distances as percentages of each watercourse's total length in the ecoregion. Second, we employed the average of these five undammed percentages as the ecoregion's undammed percentage, which ranges between 0% and 100%, where 100% denotes a free-flowing ecoregion, and a value less than 50% is referred to as a *heavily obstructed ecoregion*. Our metric reflects seemingly counter-intuitive cases of dam distribution, such as dam-dense ecoregions that retain relatively long undammed watercourses (e.g., the Lower Yangtze has more than 250 dams but an average of 77% of its watercourse length is free flowing) and ecoregions that contain few watercourses but that are highly obstructed by only a few dams (e.g., the Lower and Middle Indus Basin contains only about 20 dams but less than 50% of its watercourse length is free flowing). An informal analysis of the importance of sample size revealed that five watercourses per ecoregion was a sufficient number to allow a global assessment within the project's duration and to capture the fragmentation of mainstems and major tributaries in the ecoregions. We are confident that the extent of obstruction affecting the majority of an ecoregion's riverine

biota is captured by these five watercourses, since species richness typically increases with river size (Xenopoulos et al. 2005) and longer watercourses in general also tend to be the largest in terms of volume and discharge.

Our obstruction metric represents the degree of blockage to migration only within ecoregions, but diadromous fishes may travel between several hydrologically connected ecoregions. To address this issue, we identified ecoregions marked by downstream dam obstruction (appendix S1, column B) as a further indication of potential threats to diadromous species posed by dam obstruction. Given the availability of data, this identification is a reasonable global-scale surrogate for measuring the distance from ocean to the first dam on every watercourse entering an upstream ecoregion. It highlights the ecoregions that are most likely to be inaccessible to diadromous species and provides insight into the threats posed to potomadromous fishes as well. In addition, in order to identify the cases of neighboring ecoregions with grossly disparate degrees of dam obstruction, we tested the degree of spatial autocorrelation, using Moran's I (Moran 1950).

The lengths of the watercourses within 34 of the ecoregions were difficult to assess because of channel intermittency. Dams were present in 30 of these ecoregions, and the maximum possible lengths were recorded so that our obstruction results would be as conservative as possible (i.e., free-flowing percentages would be maximized). The relative variability in unobstructed length among the sampled watercourses differed among the ecoregions (appendix S1), and there were several cases in which the average unobstructed distance

was dominated by a single watercourse. Extensive canals or aqueduct systems were found in 25 of the ecoregions, but the roles that the canals and aqueducts in these ecoregions play for biota relative to dam obstruction is yet unknown. Waterfalls may present natural obstructions to dispersal, but the presence of migratory species provides evidence that waterfalls are not complete obstacles, and as such, the lack of global data on waterfalls did not deter our analyses. Some fish species have evolved the capacity to climb natural waterfalls (Blob et al. 2006), whereas others are stopped even by modest riffles (Lonzarich et al. 2000).

Analysis of the threat posed by dam obstruction to global fish diversity

Fish species lists were provided by the World Wide Fund for Nature (Abell et al. 2008) and represent the most comprehensive spatial data set on global freshwater fish distributions. The lists for each ecoregion include the total number of species as well as the numbers of endemic and diadromous species (Abell et al. 2008). *Endemism* is defined at the ecoregional scale. *Diadromy* refers to any species with requirements that include both freshwater and marine habitats (as derived from FishBase; www.fishbase.org), which implies obligate migratory behavior. The lists are intended to exclude introduced species, undescribed species, and confirmed extinct species but do include extirpated species in order to indicate restoration opportunities. The data quality varied: The challenges inherent to taxonomy and species concepts introduce uncertainty, and the species lists for several regions were biased by limited sampling. Despite these challenges, we argue that these uncertainties are not substantial enough to reform any emergent global patterns.

On the basis of the literature and expert opinion, we initially compiled a list of several other traits for a robust analysis of fishes particularly threatened by dam obstruction. For example, the effects on potamodromous and nonendemic fishes have been reported in the literature (e.g., Winston et al. 1991). However, such data are not available in a globally and taxonomically consistent data set, which elicited our decision to focus on obligate diadromy and ecoregional endemism, for which data were presented by Abell and colleagues (2008). We explored the distribution of species numbers (total species richness, counts and percentages of endemic and diadromous species) in relation to free-flowing distance. Recognizing the limitations of the available data (temporal and spatial resolution) for exploring causal relationships between dams and current fish distributions, we focused on graphical approaches to identifying ecoregions at risk of species loss and avoided explanatory models. We describe gradients of risk and related conservation or restoration potential on the basis of the degree of dam obstruction and relative species richness, percentage endemism, and percentage diadromy. We consider *conservation* to be the maintenance of a current state or system and *restoration* to be the initiation of its recovery to a more natural state.

Assessment of habitat alteration

In addition to the landscape-scale threat posed by dams, freshwater habitat alteration within ecoregions is a local-scale risk factor for native species loss, the degree of which serves to further identify where and how protection and restoration actions may be prioritized. Because globally consistent spatial data on freshwater habitat alteration are unavailable, we used the percentage of urban and agricultural land conversion within an ecoregion (1-kilometer spatial resolution; Hansen et al. 2000) as a surrogate. The areas dominated by humans (urban and agricultural) are likely to be the areas where flow and thermal regimes are most altered and where habitat for native freshwater species is most likely adversely altered (Okamura and Feist 2011). Although globally consistent high-resolution spatial data are not available to capture many other small-scale land conversions shown to alter freshwater habitat, such as timber harvest, the data set is expected to capture these land uses within the agricultural class if they extend a minimum of 1 square kilometer. However, because the data set groups some forms of pastureland with natural vegetation, varying percentages of pastureland were not considered because of a desire to systematically under- rather than overestimate habitat alteration and to ensure that the results err on the conservative side. The final estimates of the amount of altered habitat were then considered in tandem with fish data (species richness, endemism, diadromy) for each ecoregion to identify the risk of species loss and conservation or restoration potential.

Mapping dam obstruction

Sufficient data on dam obstruction were available for 397 freshwater ecoregions (excluding Antarctica; see figure 1 and appendix S1). The dam data were insufficient for 50 ecoregions—mostly small islands and portions of the Middle East. Dams were not found on the five longest watercourses in 137 ecoregions. Dam-obstructed ecoregions dominate North America and Europe and are strongly evident in Asia (figure 1), which parallels the patterns found at basin resolution in previous studies (Dynesius and Nilsson 1994, Nilsson et al. 2005). Except for the humid Amazonian ecoregions, negligibly obstructed ecoregions tend to dominate arid parts of the world (e.g., central Asia, northern Africa, Australia, the tundra of North America). One hundred forty ecoregions are connected to at least one downstream ecoregion, 106 of which face obstruction in at least one of those ecoregions. Of the 21 most heavily obstructed ecoregions whose watercourse distance is less than 50% free flowing, 8 (Columbia Glaciated, English–Winnipeg Lakes, the Great Lakes, the Mississippi, the Southern Temperate Highveld, Teays–Old Ohio, the Upper Danube, and the Upper Paraná) face additional obstruction in downstream ecoregions. An analysis of spatial autocorrelation (Moran's I) indicated strong clustering of dam obstruction among ecoregions ($p < .01$), which suggests that cases of hydrologically connected ecoregions hosting disparate degrees of dam obstruction are few.

Dam obstruction and global fish diversity

Species richness data were available for 397 ecoregions, whereas reliable data for endemism and diadromy were available for 393 and 391 ecoregions, respectively. The top five ecoregions in terms of species richness are in the Amazon, and they generally remain unobstructed (figure 2). Other species-rich ecoregions that remain unobstructed exist in central Africa (e.g., the upper Nile, the upper Congo, Cuvette Centrale), the Upper Yangtze and Salween in mainland Asia, and many Indonesian and Malaysian ecoregions. Some of the largest unobstructed ecoregions coincide with arid, species-poor parts of the world (e.g., ecoregions in western Australia, northern Africa, central Asia, and the tundra of North America and northern Asia). Ecoregions with the highest percentage of endemic species tend to be lakes and island systems, such as the unobstructed Lake Lanau ecoregion in south Asia, where all 16 fish species present are endemic. The top 15% scores ($n = 61$) for the percentage of diadromy are all for ecoregions with more than 50% of their distance free flowing, with leading scores for island ecoregions such as the Hawaiian Islands, Greenland, Puerto Rico, and Madagascar. Whereas total species counts and the percentages of endemism and diadromy each encompass the entire range of values among the least obstructed ecoregions, these values are invariably low among the ecoregions with lower percentages of free-flowing watercourse distance (figure 3). Of ecoregions with above-average values for either measure of species richness—percentage of endemism or of diadromy—we considered 50% free-flowing distance as the threshold below which we refer to ecoregions as having high

restoration potential or as restoration priorities. Eighteen of the 21 heavily obstructed ecoregions meet these criteria (table 1), and half of them support higher-than-average species richness and either a higher percentage endemism or a higher percentage diadromy: Mobile Bay, the South Atlantic region of the United States, the North Atlantic, Sabine–Galveston, the Laurentian Great Lakes, the Upper Paraná, the Dniester–Lower Danube, West Korea, and the Lower and Middle Indus Basin. Southern Italy (which is also heavily obstructed) is a unique case in that it is relatively species poor but supports higher-than-average percentages of diadromy and endemism. Nineteen ecoregions remain 100% free flowing, and support both higher-than-average species richness and either percentage endemism or percentage diadromy. There are eight relatively species-poor unobstructed ecoregions that support above-average percentages of both endemism and diadromy.

Taxa at risk

We examined the distribution of diadromy and endemism among heavily obstructed ecoregions (tables 1 and 2). The taxa cited include genera with many migratory species, particularly eels (*Anguilla* spp.) and shads (*Alosa* spp.), for each of which diadromy constitutes over 75% of the species found in heavily obstructed ecoregions. Although they are globally widespread, 77% of the eel species found in the 21 most heavily obstructed ecoregions (and more than 20% of the species worldwide) are diadromous, which renders them particularly vulnerable to dam obstruction. *Lampetra* species face a perhaps greater threat in that there are only 55 species of lamprey worldwide, 11% of their distribution (10

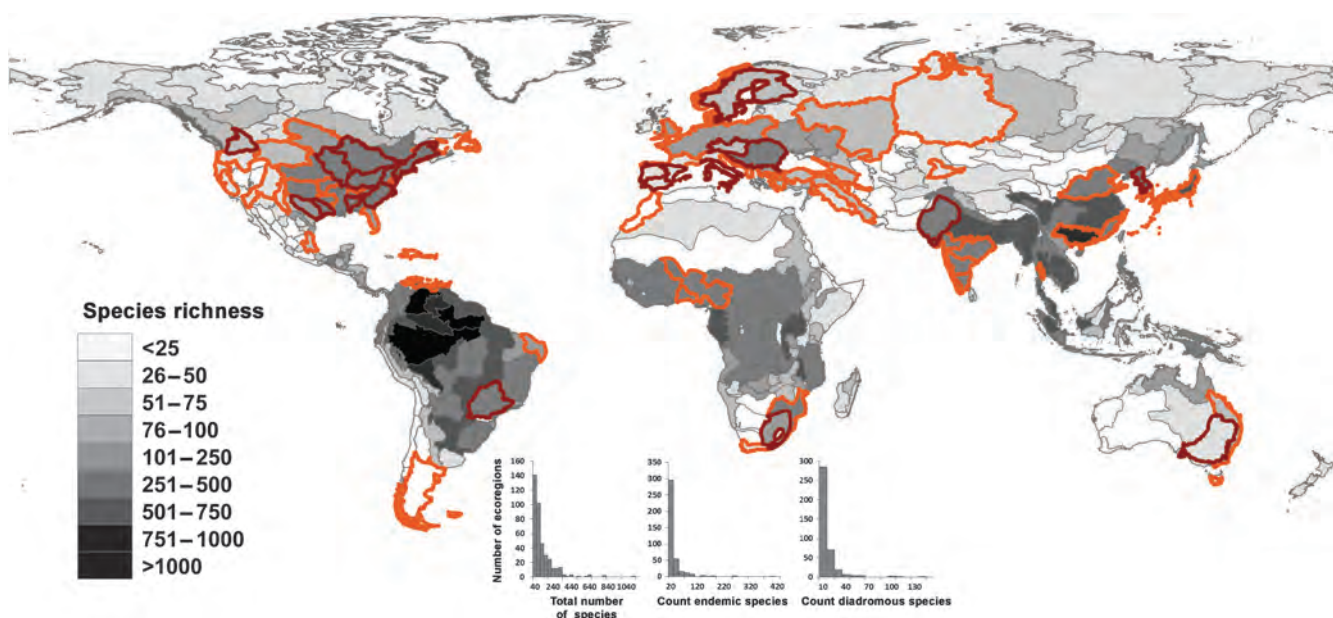


Figure 2. Fish species richness among freshwater ecoregions. The ecoregions whose longest watercourses distances were on average less than 50% free flowing are outlined in red, and those with 50%–75% are outlined in orange. The graphs show the frequency distributions of fish species richness ($n = 397$), endemism ($n = 393$), and diadromy ($n = 391$). The data are positively skewed, with most ecoregions harboring relatively low counts of total, endemic, and diadromous fish species.

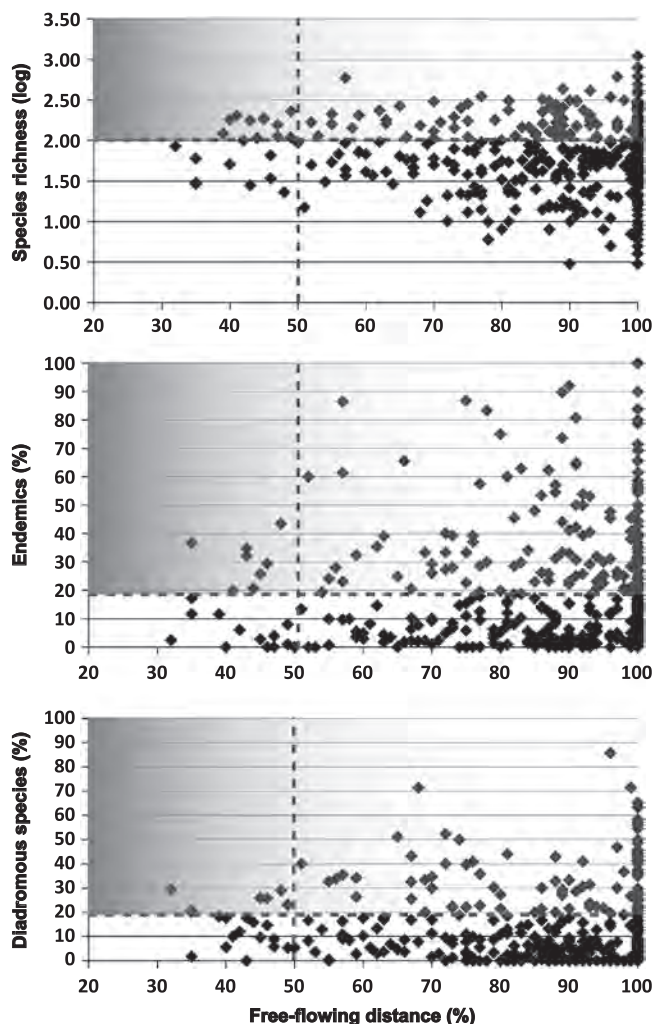


Figure 3. Fish species richness ($n = 397$), percentage of endemic species ($n = 393$), and percentage of diadromous species ($n = 391$) relative to unobstructed watercourse length among freshwater ecoregions. The horizontal dashed lines indicate the mean values; the vertical dashed lines indicate that 50% of the watercourse distance is free flowing. The shaded areas represent the gradient from restoration to conservation potential. The darkest gray areas in the upper left portions of the plots indicate the highest-priority ecoregions for river restoration, with high species values and relatively low percentages of free-flowing distance. The lighter gray areas in the upper right portions of the plots represent priority ecoregions for river conservation, with both high species values and more than 50% of its remaining distance as free flowing.

of 90 ecoregions) is heavily obstructed, and 28% (5 of 18) of the *Lampetra* species found in heavily obstructed ecoregions are diadromous. Sturgeons (*Acipenser* spp.) and salmonids (*Salmo* and *Onchorynchus* spp.) are other highly diadromous genera facing impacts from heavy dam obstruction. About

11% (4 of 37) of the sculpins (*Cottus* spp.) are endemic, which renders those species particularly vulnerable to loss in the heavily obstructed ecoregions (table 2).

Compounding threats

The mean level of habitat alteration for the ecoregions, indicated by urban or agricultural land use, was 10% (standard deviation = 11.67) and ranged from 0% to 67% (appendix S1). Five of the ecoregions were dominated (more than 50%) by altered habitat—the Bonaerensean Atlantic Drainage, Central Europe, the Dniester–Lower Danube, Dnieper and South Bug, and Crimea—whereas at least 25% of the 35 additional ecoregions face habitat alteration.

Southern Italy is relatively species poor, with high percentages of endemism and diadromy, coupled with more than 30% habitat alteration (the Murray–Darling Province presents a similar situation). The Lower and Middle Indus Basin hosts above-average species richness and 27% diadromous species, with the highest counts of diadromy ($n = 50$) among heavily obstructed ecoregions, and its habitats remain relatively unaltered (16%). The Upper Danube is possibly the most extreme case of compounded threats, because it is heavily obstructed by dams and affected by land use and lies upstream of a similarly degraded ecoregion (the Dniester–Lower Danube, which is 39% free flowing and has more than 50% altered habitat); the total, endemic, and diadromous species values for this ecoregion, however, are below average. South China presents the most species-rich ecoregion ($n = 549$) to also face serious dam obstruction (less than 60% remains free flowing) and altered habitat (37% of the region is urban or agricultural). Lake Tana, the Nile Delta, and Inle Lake are all unobstructed ecoregions with more than 25% altered habitat. Both Lake Tana and Inle Lake support above-average levels of endemism, and the Nile Delta has an above-average level of diadromy.

At least six of the 18 restoration-priority ecoregions encompass or overlap the basins predicted by Xenopoulos and colleagues (2005) to lose 10% or more of their fish species by the 2070s because of changes in climate or water withdrawal (table 1). These regions include Southern Italy, Sabine–Galveston, the Murray–Darling Province, Central Iberia, Southern Iberia, and the Southern Temperate Highveld.

Conclusions

In this study, we present the first globally comprehensive analysis of fragmentation by dams in relation to freshwater fish distributions, and we identified ecoregions and freshwater fish taxa at particular risk of species loss because of the effects of dam obstruction. The maps and analytical results provide spatial and taxonomic information for application in freshwater research and management, including the international prioritization of freshwater habitat conservation and restoration, and are a response to recent calls for identifying the freshwater systems most in need of protection (Abell et al. 2007) during a noted freshwater biodiversity crisis. Dams have been pinpointed as one of the threats—if

Table 1. Fish species statistics for the 18 ecoregions for which less than 50% of the average watercourse was free flowing and that had above-average values for species richness, endemism, or diadromy.

Ecoregion	Average percentage of unobstructed watercourse	Total number of fish species	Endemism		Diadromy	
			Number of species	Percentage	Number of species	Percentage
Teays–Old Ohio	49.03	228	18	8	12	5
North Atlantic	48.80	109	1	1	26	24
Southern Italy ^a	47.66	23	10	43	9	39
Laurentian Great Lakes	46.92	156	6	4	19	12
Sabine–Galveston ^a	46.63	113	0	0	10	9
Columbia Glaciated	46.14	66	0	0	18	27
Murray–Darling Province ^a	46.05	34	10	30	5	15
Lower and Middle Indus Basin	45.47	182	5	3	50	27
South Atlantic	45.38	187	48	26	18	10
West Korea	44.49	107	22	21	17	16
Central Iberia ^a	43.30	28	9	32	5	18
Upper Paraná	43.19	176	61	35	0	0
East Texas Gulf	41.85	100	6	6	12	12
Mobile Bay	41.46	202	40	20	20	10
Mississippi	39.82	180	0	0	10	6
Dniester–Lower Danube	38.51	121	14	12	24	20
Southern Iberia ^a	35.40	30	11	37	6	20
Southern Temperate Highveld ^a	31.90	85	2	2	25	29
Global mean		100	18	19	8	18

Note: The ecoregions are listed in descending order of remaining unobstructed watercourse. The counts above the global means are in bold.

^aEcoregions that overlap the basins predicted by Xenopoulos and colleagues (2005) to lose 10% or more fish species by the 2070s because of changes in climate and withdrawal scenarios.

not the strongest threat—to freshwater biodiversity at the global scale (Vörösmarty et al. 2010), which highlights the value of this study's results for slowing species losses.

For the ecoregions with above-average counts of species or percentages of endemism or diadromy, we considered 50% free-flowing distance to be the threshold below which we identified the ecoregions as having high restoration potential or to be restoration priorities and above which is drawn a gradient from restoration to conservation potential (figure 3). This threshold (and that of mean species count values) can, of course, be shifted according to individual interpretation but provides a useful framework for discussing restoration and conservation potential. Far fewer ecoregions meet the restoration-priority criteria than lie toward the conservation end of the spectrum (figure 3). Although restoration is often expensive, this relatively low number of restoration priorities may increase the likelihood of restoration projects' receiving funding. Many river-restoration plans have proven successful in their targeted goals (see Bernhardt and colleagues [2005] for a comprehensive list of river restoration possibilities and Palmer and colleagues [2008] for management actions appropriate to dammed basins) and may include dam reoperation, modification (such as the addition of a fish passage) or removal, or environmental flow management.

Of the 18 restoration-priority ecoregions (table 1), 8 face additional threats either by more than 25% habitat alteration or by additional downstream dam obstruction (appendix S1; Columbia Glaciated, the Laurentian Great Lakes, the Mississippi, Teays–Old Ohio, the Upper Paraná, Southern Italy, the Upper Danube, and the Southern Temperate Highveld). These eight ecoregions may be in the most immediate need of management action to stave off species losses, with actions chosen according to species and channel characteristics (e.g., the availability of spawning ground upstream of dams). Because some pastureland is excluded from the landcover categories used in our habitat-alteration analysis, the alteration values for pasture-dense ecoregions (e.g., New Zealand) are particularly conservative, which suggests that habitat alteration may compound threats posed by dams in more heavily obstructed ecoregions than those highlighted here. Heavy habitat alteration may also warrant restoration or conservation action in unobstructed ecoregions, especially those with high species values, such as Lake Tana, Inle Lake, and the Nile Delta. A 10% or greater loss applied to relatively species-poor ecoregions with high percentages of endemism may markedly impact regional or even global biodiversity (e.g., Southern Italy, in which 10 of the 23 species [43%] are endemic). The Murray–Darling Province, Central Iberia, and Southern Iberia ecoregions

Table 2. Diadromy and endemism among the most prevalent genera of the most heavily obstructed ecoregions.

Genus	Common name	Number of heavily obstructed ecoregions in which the genus is cited	Number of diadromous species	Number of endemic species	Total number of species
<i>Anguilla</i>	Eels	18	17	0	22
<i>Alosa</i>	Shads	14	25	1	32
<i>Esox</i>	Pickerels and pikes	12	0	0	24
<i>Acipenser</i>	Sturgeons	11	9	0	20
<i>Cottus</i>	Sculpins	11	2	4	37
<i>Gasterosteus</i>	Sticklebacks	11	1	0	13
<i>Phoxinus</i>	Dace	11	0	1	18
<i>Salmo</i> , <i>Onchorynchus</i>	Trouts and salmonids	11	6	1	18
<i>Ameiurus</i>	Bullheads	10	0	1	27
<i>Lampetra</i>	Lampreys	10	5	0	18
<i>Lepomis</i>	Sunfish	10	0	0	60
<i>Micropterus</i>	Bass	10	0	0	22
<i>Perca</i>	Perches and darters	10	0	0	10

Note: The genera are listed in decreasing order of prevalence. Those with high counts of diadromy or endemism are particularly vulnerable to the effects of dam obstruction.

are similar cases. Species in these ecoregions on which dam obstruction has an impact and that are projected to lose species because of future discharge regimes (table 1) are facing a greater level of extinction risk relative to species elsewhere.

Immediate management action is prudent, not only for the ecoregions and taxa identified as at the greatest risk from dams but also for the half of the world's freshwater ecoregions that remain relatively unobstructed. When the gradient from restoration to conservation potential (figure 3) is considered, a far greater number of ecoregions lie toward the conservation end of the spectrum, which highlights a strong potential to curb further freshwater species losses globally. Conservation plans for these relatively unobstructed ecoregions may become more critical as climate change and population growth increase the demands placed on freshwater systems (Palmer et al. 2008); indeed, dam construction currently progresses worldwide at alarming rates in attempts to meet these demands. The creation or expansion of freshwater protected areas, development of integrated catchment management plans, and environmental flow prescriptions represent strategies with high potential for both conservation and restoration (Abell et al. 2007, Arthington et al. 2010, Linke et al. 2011). Considering ecoregions in this context could assist planners with decisions to remove, rebuild, or construct dams by helping to elucidate the trade-offs associated with each decision (Kareiva et al. 2007).

The increasing range of species counts visible along the gradient of free-flowing portions of the watercourse (figure 3) raises questions about the ability of more heavily

obstructed ecoregions to maintain higher species diversity. One explanation may be that dam impacts have been positively correlated with human economic activity (Nilsson et al. 2005), and humans have preferentially settled in the temperate regions that are inherently less species diverse than tropical or subtropical regions. Regardless, in terms of dam obstruction alone, the least-obstructed ecoregions represent notable opportunities for biodiversity conservation.

Although an examination of the cause-effect relationships between dam obstruction and freshwater species distributions was not a focus of this study, it is important to note that such analyses would suffer from data deficiency. For example, there is no complete global database for dams (Lehner et al. 2011), but gaps in the data concern mostly small dams, whereas the majority of the world's nearly 50,000 large dams (whose dam height exceeds 15 meters) are

included. The absence of data on small dams highlights the important point that the cumulative effects of many small dams can differ from and even exceed those of a single large dam. Existing data sets frequently miss dams for reasons as varied as political or regional focus. Many dams that could be digitally georeferenced were manually added to existing data sets for use in this study, but many dams without locational data remain omitted. For example, the International Commission on Large Dams refers dams to the nearest city, which, in sparsely populated regions, may suggest a different river. Data on the number of fish that pass a dam are not available globally, which highlights the need for managers to examine higher-resolution data before choosing management actions.

Similar inconsistencies exist for the fish data, but fish still represent the group of globally well-distributed freshwater organisms whose occurrences are best known. It is important to reiterate that the global data for fish species distribution summarized herein vary spatially in quality and certainty and may differ from locally derived data. In particular, Abell and colleagues (2008) noted likely underestimates of the total number of species caused by the authors' conservative approach in data validation and possible overestimates of endemic species because endemics were identified through a query for unique occurrences among species lists that may be incomplete or in which synonyms may have been used. The globally available data on diadromy do not include inter- and intraspecific differences in the ability of fish to pass obstacles, which again suggests that managers should

examine more detailed data before choosing management actions for a given ecoregion. Furthermore, the fish diversity data include extirpated species, and therefore, many species cited in the heavily obstructed ecoregions could be either threatened by extinction or lost. For example, many dams are younger than the generation times of some fish species—in most cases, less than five decades (WCD 2000)—which makes the presence of an extinction debt (*sensu* Tilman et al. 1994) quite likely. Nonetheless, the global scale allows for the identification of relative differences, which provides operational value in terms of conservation, restoration, and research planning. Global lists are being updated but are far from complete. For example, the International Union for Conservation of Nature produces tentative lists of species at risk, from *least threatened* to *extinct* (IUCN 2010), but their limited spatial and temporal resolution restricts their utility for global-scale analyses. Several sources, in addition to the data used in this study, are advancing the spatial, taxonomic, and temporal extent of freshwater fish data (e.g., the United Nations' World Conservation Monitoring Center [Groombridge and Jenkins 1998], FishBase [www.fishbase.org], BioFresh [www.freshwaterbiodiversity.eu] and an independently constructed data set addressing the distribution of invasive species [Leprieur et al. 2008]), but taxonomic, spatial, and temporal data gaps still remain, which prevents detailed quantitative global analyses.

Through this analysis, we assume that the dams on the five longest channels within an ecoregion indicate the degree of dam obstruction within the entire ecoregion. There may be exceptions to this premise—for example, for ecoregions with a dense distribution of dams among small headwaters or near the river mouth but with largely free-flowing main-stem rivers. In such cases, however, the level of obstruction affecting the majority of the riverine biota would still be captured, since fish species richness typically increases with river size (Naiman et al. 1987, Xenopoulos et al. 2005), and the five longest measured watercourses are also likely to have the greatest discharge. Most ecoregions are not equivalent to river catchments, and therefore, the routed, cumulative effects of river obstruction within individual catchments cannot be assessed at the ecoregional scale. The transport of water, sediments, and nutrients may already be obstructed by dams in rivers originating in an upstream ecoregion, despite the ecoregion in question's having few or no dams. Fish migration may also be blocked by dams in an ecoregion downstream. Such issues are difficult to disentangle, because doing so would require a redelineation of the ecoregions by hydrology, which defeats their purpose as biologically defined spatial units, in some cases longitudinally distinct within a river basin but in others comprising several catchments. However, our identification of ecoregions facing downstream obstruction (appendix S1) and the analysis of spatial autocorrelation address the issue of fish migration blocked by neighboring ecoregions. Nonetheless, recognition of these external dam-related threats delivered to ecoregions reinforces the need to consider the results of this

study as minimums when considering the dam-related threats to freshwater species richness.

In summary, we have identified the ecoregions most at risk of species loss because of dam obstruction, as well as ecoregions facing additional threats from habitat alteration, external dams, and future changes in water availability. The diadromous and endemic taxa found in these most-threatened ecoregions are identified as at particular risk (table 2) and merit immediate conservation attention. The gradient from restoration to conservation potential provided in figure 3 and linked to appendix S1 allows the international community to prioritize not just management but additional higher-resolution research as well.

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