Fragmentation and Flow Regulation of the World's Large River Systems

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A global overview of dam-based impacts on large river systems shows that over half (172 out of 292) are affected by dams, including the eight most biogeographically diverse. Dam-impacted catchments experience higher irrigation pressure and about 25 times more economic activity per unit of water than do unaffected catchments. In view of projected changes in climate and water resource use, these findings can be used to identify ecological risks associated with further impacts on large river systems.

Humans have extensively altered river systems through impoundments and diversions to meet their water, energy, and transportation needs. Today, there are >45,000 dams above 15 m high, capable of holding back >6500 km^3 of water (*1*), or about 15% of the total annual river runoff globally (*2*). Over 300 dams are defined as giant dams, which meet one of three criteria on height (>150 m), dam volume (>15 million m^3), or reservoir storage (>25 km^3) (*3*). The recently constructed Three Gorges Dam on the Chang Jiang (Yangtze) in China is the largest, 181 m high and with a reservoir storing >39 km^3 (*4*, *5*). Although statistics summarizing the world's large dams are available (*3*, *4*, *6*, *7*), detailed multiscale data have not been synthesized globally.

Catchment-scale impacts of dams on ecosystems are generally well known, with both upstream and downstream effects stemming from inundation, flow manipulation, and fragmentation (*8–10*). Inundation destroys terrestrial ecosystems and eliminates turbulent reaches, disfavoring lotic biota. It can cause anoxia, greenhouse gas emission, sedimentation, and an upsurge of nutrient release in new reservoirs (*6*, *11*, *12*). Resettlement associated with inundation can result in adverse human health effects and substantial changes in land use patterns (*13*, *14*). Flow manipulations hinder channel development, drain floodplain wetlands, reduce floodplain productivity, decrease dynamism of deltas, and may cause extensive modification of aquatic communities (*15–18*). Dams obstruct the dispersal and migration of organisms, and these and other effects have been directly linked to loss of populations and entire species of freshwater fish (*19–21*). The World Commission on Dams produced the most comprehensive review of dam impacts yet (*22*), with illustrative catchment-scale case studies. However, data were not available for a global analysis based on subcatchment-scale resolution, integrating hydrologic, ecological, and socioeconomic data. Such a synthesis is needed to understand the multiple spatial, temporal, and interactive impacts of dams.

Here, we present a global overview of flow regulation and channel fragmentation in the world's largest river systems, which comprise a total virgin mean annual discharge (VMAD, the discharge before any substantial human manipulations) of some 790,000 m^3 s^{-1}, or 60% of the world's river runoff. We proceeded by (i) identifying 153 large river systems (LRSs) in Latin America, Africa, Asia, and Australasia that we had not previously assessed (*23*), (ii) locating and gathering storage capacity data for their dams, (iii) quantifying channel fragmentation by dams, (iv) and quantifying flow regulation by relating storage capacity to discharge. We also updated these same data for 139 systems that we had previously assessed in the Northern Hemisphere (*23*), combined the two data sets for a total of 292 river systems, and, on the basis of these data, classified the river systems as either unaffected, moderately affected, or strongly affected (*24*). We were unable to assess rivers in most of Indonesia and a small part of Malaysia (because of a lack of reliable discharge data). We included irrigation data for all 292 LRSs and analyzed global distribution of impact relative to terrestrial biomes and economic activity.

We defined an LRS as a system that has, anywhere in its catchment, a river channel section with a VMAD of ≥350 m^3 s^{-1} (*23*, *25*). By river system, we mean entire networks of stream and river channels interconnected by surface freshwater, from the headwaters to the sea (*26*). The 292 LRSs (table S1 and Fig. 1) drain 54% of the world's land area. North and Central America contain more LRSs (88 total) than any other continent, but on average these systems contribute less water and have smaller catchment areas than do those of Asia, Africa, and South America. Of the 10 LRSs with highest discharge, 6 lie in Asia, 2 in South America, 1 in Africa, and 1 in North and Central America.

The catchments of LRSs encompass at least some part of all 16 of the world's nonmarine biomes as classified by Olson *et al*. (*27*) and >50% of 11 of these biomes, including 87% of all boreal forests and 83% of all flooded grasslands and savannahs. The biomes with least proportion of their surface area in LRSs are rock and ice (1%); mangroves (17%); and Mediterranean forests, woodlands, and scrub (19%). In all, 72 LRSs span only one biome, whereas the Ganges-Brahmaputra system (AS-65) encompasses the widest diversity (10 biomes), followed by the Amazonas-Orinoco (SA-11; these rivers have a natural cross-channel), Amur (AS-20), Yenisei (AS-5), Zambezi (AF-6), and Indus (AS-73) systems, each spanning eight.

Nearly half (139) of all LRSs (48%) remain unfragmented (*28*) by dams in the main channel, 119 systems (41%) have unfragmented tributaries, and 102 systems (35%) are completely unfragmented. Europe contains the smallest number of completely unfragmented LRSs (just three rivers in northwestern Russia). The continent with the greatest number (35) of unfragmented LRSs is North and Central America, and the greatest proportion is in Australasia (74%). Twelve LRSs (9 in Europe and 3 in the United States) have <25% of the main channel's length left unfragmented.

The greatest flow regulation (*29*) was for the Volta river system in Africa (AF-19, 428%). In North and Central America, both the Manicougan (NA-35) and Colorado (NA-70) systems are regulated >250%, and in South America the most highly regulated system is the Rio Negro in Argentina (SA-22, 140%). The most highly regulated systems in Asia are the Shatt Al Arab (or Euphrates-Tigris) in the Middle East (AS-74, 124%) and the Mae Khlong in Thailand (AS-58, 130%). Flow regulation does not exceed 100% in any LRS in Europe or Australasia. A flow regulation of 100% indicates that the entire discharge of one year could be held back and released by the dams in the river system.

The numbers of unaffected and strongly affected LRSs are roughly equal (120 and 104, respectively), whereas moderately affected systems represent just 23%, or 68 of the 292 LRSs (Fig. 1). Of the 10 LRSs with highest discharge, 6 are moderately affected and 4 are strongly affected. The world's two largest discharges, the Amazonas-Orinoco and Congo, are moderately affected, and the third largest discharge, the Chang Jiang, is strongly affected (table S1). The largest unaffected LRS is the

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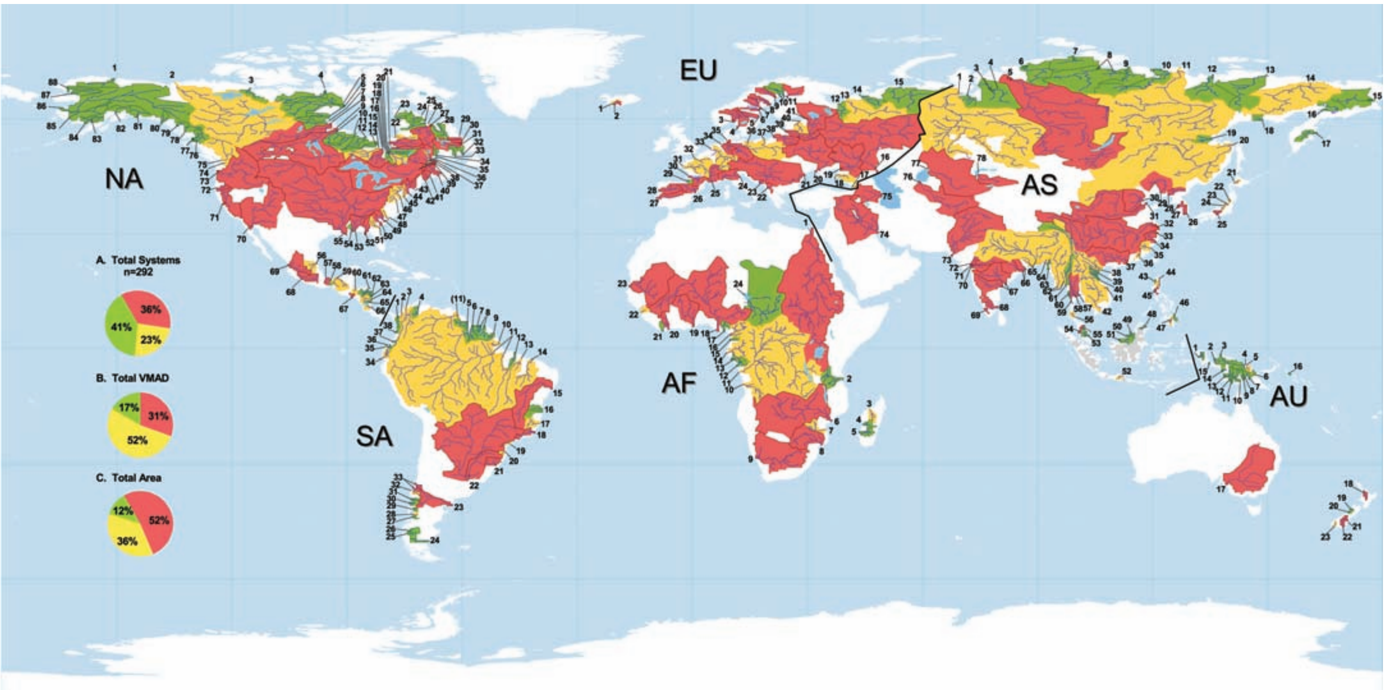

Fig. 1. Impact classification based on river channel fragmentation and water flow regulation by dams on 292 of the world's large river systems. River systems are treated as units and are represented on the map by their catchments. Numbers refer to the list of LRSs in table S1. Green, yellow, and red indicate unimpacted, moderately impacted, and strongly impacted catchments, respectively. White areas indicate land not covered by LRSs. Systems excluded from the study for lack of data are shown in gray. Diagrams at left show A, total number of LRSs; B, total VMAD of LRSs; and C, total surface area of LRSs. NA, North and Central America; SA, South America; AF, Africa; EU, Europe; AS, Asia; AU, Australasia.

Yukon (22nd highest VMAD). Strongly affected systems constitute the majority (52% or 41.2×10^6 km^2) (Fig. 1) of total LRS catchment area, despite contributing less water per system (2326 m^3 s^{-1}) and per system catchment area (396×10^3 km^2) than moderately affected LRSs. Among continents, the highest number (40) of unaffected LRSs is in North and Central America, whereas Australasia contains the highest proportion (74%) of unaffected systems. Europe has both the smallest number (five) and smallest proportion (12%) of unaffected LRSs (Fig. 2).

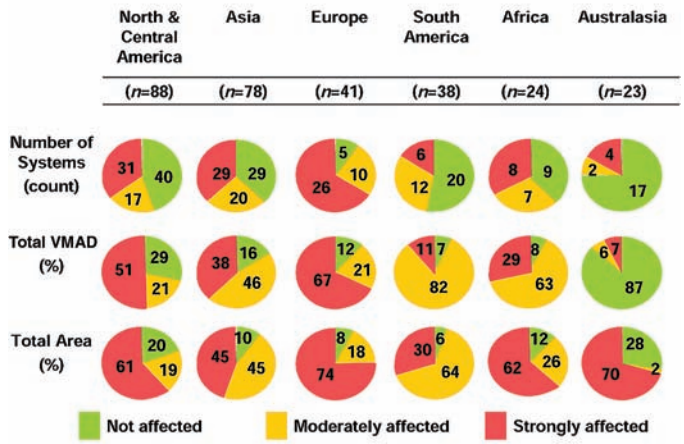

Fig. 2. Total number of systems, total water discharge, and total basin area of strongly affected, moderately affected, or unaffected within each continent's LRSs. Percentages may not total 100% because of independent rounding.

Fourteen unaffected or moderately affected LRSs nearly meet fragmentation and regulation criteria for higher impact classification (NA-14, 47, 48, 54, and 80; SA-28 and 32; EU-18, 29, and 33; and AS-1, 24, 35, and 36). Small increases in flow regulation caused by irrigation could change these classifications. Although many dams provide water for irrigation, nonreturned withdrawal from a river's flow for irrigation is a separate and additional form of flow regulation to that caused by retention and release of water by dams. To assess this, we constructed an irrigation index representing the area equipped for or under irrigation (*30*) within each LRS per unit of water in the system (table S1).

Strongly affected systems account for the 25 highest irrigation index values, 15 of which lie in Asia, with the Haihe in China (AS-30) scoring the highest (2194 km^2 per annual km^3 of discharge) (table S1). Of the five borderline unaffected systems, index values only suggest reclassification (to moderately affected) for the Adour in France (EU-29). Of the nine borderline moderately affected systems, index values were high enough to suggest reclassification (to strongly affected) for five systems: Bío-Bío in Chile (SA-32), Kuban in western Russia (EU-18), Agano-Gawa in Japan (AS-24), and Min Jiang and Han Jiang in China (AS-35 and 36, respectively).

Most of the unaffected LRSs are situated in just four biomes (tundra; boreal forests; tropical and subtropical moist broadleaf forests; and tropical and subtropical grasslands, savannahs, and shrublands) (Fig. 3), constituting small proportions of each biome. Tundra, which is sparsely populated, relatively flat, and thus unfavorable to dam construction, is the only biome in which LRS catchment area (29% of total biome area) is predominantly unaffected (73%). Even if unassessed river systems are assumed to be unaffected (a best-case scenario), the maximum proportion of unaffected biome area is still <40% for each of boreal forests; tropical and subtropical moist broadleaf forests; and tropical and subtropical grasslands, savannahs, and shrublands.

Catchment area of strongly affected LRSs constitutes >50% of three biomes (temperate

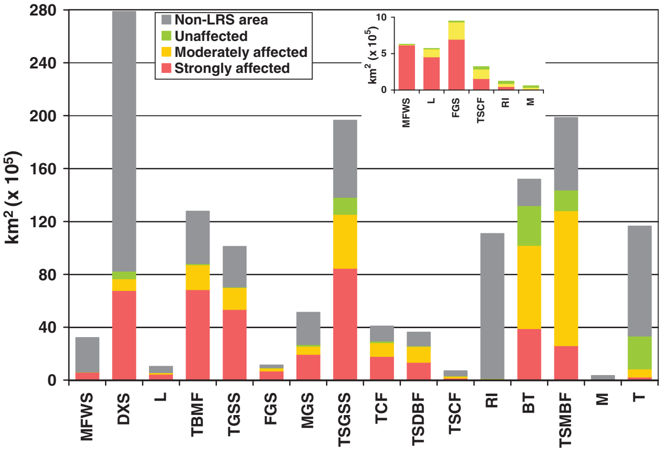

Fig. 3. Distribution of surface area within each of the world's 16 nonmarine biomes among the catchments of unaffected, moderately affected, or strongly affected LRSs; gray represents a non-LRS area, including potential LRSs in Indonesia and Malaysia. Biomes are listed in descending order from left to right by proportion of strongly affected area within LRS-covered area. (**Inset**) Increased resolution of impact class distribution for six biomes with little LRS-covered area. MFWS, Mediterranean forests, woodlands, and scrub; DXS, desert xeric shrubs; L, lakes; TBMF, temperate broadleaf mixed forests; TGSS, temperate grasslands, savannahs, and shrublands; FGS, flooded grasslands and savannahs; MGS, montane grasslands and shrublands; TSGSS, tropical and subtropical grasslands, savannahs, and shrublands; TCF, temperate conifer forests; TSDBF, tropical and subtropical dry broadleaf forests; TSCF, tropical and subtropical coniferous forests; RI, rock and ice; BT, boreal forests/taiga; TSMBF, tropical and subtropical moist broadleaf forests; M, mangroves; and T, tundra.

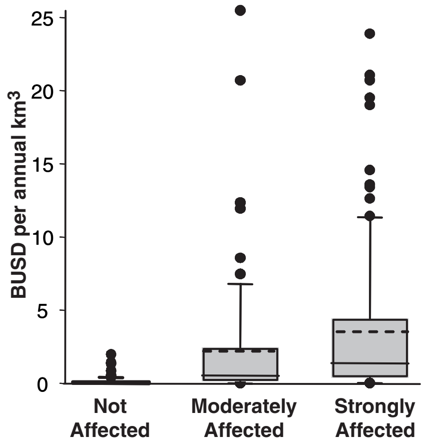

Fig. 4. Distribution of GLP [in billions U.S. dollars (BUSD)] within not affected (n = 120), moderately affected (n = 68), and strongly affected (n = 104) LRSs. Percentile divisions are 10 (not visible), 25, 50, 75, and 90; means are shown as dotted lines.

broadleaf and mixed forests; temperate grasslands, savannahs, and shrublands; and flooded grasslands and savannahs). Within the catchment area of LRSs, 82% is strongly affected in deserts and xeric shrublands, and 99% in Mediterranean forests, woodlands, and scrubs. Flow regulation, implying reduced flooding and less productive floodplains, may be especially harmful in the dry and cold biomes where species are particularly dependent on the riparian resource (*31*, *32*).

The eight LRSs that span seven or more biomes are all moderately or strongly impacted (SA-11; AS-1, 5, 20, 62, 65, and 73; and AF-6) (table S1). Of the 37 LRSs that span five or more biomes, only five remain unaffected (Catatumbo, SA-4; Salween, AS-61; Rufiji, AF-2; Mangoky AF-5; and the Chari, AF-24) (table S1). In these biogeographically diverse LRSs, the impacts of dams are more widespread than those in less diverse systems, because more ecotones are affected by fragmentation.

Moderately and strongly affected LRSs already dominate several biomes, and those biomes may become totally devoid of unaffected river systems if this pattern persists in the smaller basins and subbasins. Indeed, previous results from the Nordic countries show that the regional distribution of impact classes is similar between LRSs and small- and medium-sized river basins (*23*).

In the past century, dam construction has coincided with economic development at the national and regional scales (*22*). To examine the current state of this relationship at the basin scale, we calculated a per-discharge gross LRS product (GLP) accounting for basin population, associated national economies, and VMAD (*33*). Results show that basin impact increases with economic activity, and average GLP of unaffected LRSs is 25 times lower than that of both moderately and strongly affected LRSs (Fig. 4). There are five strongly affected LRSs with negligible GLPs [<$1 million (U.S.) km^{-3}] (table S1), all in northern Canada. These systems lie in sparsely populated regions (driving the low GLPs), and dam benefits (hydropower) are exported to other basins (*34*).

There are 46 LRSs for which large dams are planned or under construction, with anywhere from 1 to 49 new dams per basin (*35*). Forty of these LRSs are in non-OECD (Organization for Economic Cooperation and Development) member nations, indicating that future dam development does not depend on strong national economies. Almost half of the new dams are located on just four rivers, i.e., 49 on the Chang Jiang (AS-32), 29 on the Rio de la Plata (SA-22), 26 on the Shatt Al Arab (AS-74), and 25 on the Ganges-Brahmaputra (AS-65) (*35*). New dams are also planned for several unaffected LRSs, including the Jequitinhonha (SA-16), Cá (AS-40), Agusan (AS-46), Rajang (AS-51), and Salween (AS-61). For each impact class, LRSs with weak economies (*36*) experience greater per-discharge population pressure (*37*) than economically strong LRSs, contributing to greater demand for dam construction among poorer basins. As in northern Canada, interbasin exchange of dam benefits will continue to influence decisions about dam construction. For example, more than 13 dams are planned or proposed for the currently unaffected Salween, the most imminent of which (the Tasang on the main stem) aims to provide international and interbasin benefits (*38*).

As noted, we excluded from our analysis most systems in Indonesia and several in Malaysia. This is unfortunate, because the region is one of the world's top three hotspots for biodiversity (*39*). Additionally, our definition of LRS depends solely on discharge, neglecting spatially large river systems in arid regions that carry little water on an annual basis (e.g., the Rio Grande in North America). Our classification features two limitations. First, it does not address within-basin variations in impacts, which could be substantial in large basins. For example, the moderately affected Mackenzie and Amazonas-Orinoco systems include extensive, virtually pristine areas as well as strongly affected areas. Second, our data often represent minima. We stopped gathering reservoir data once a system reached classification as strongly affected (although any outstanding dams are likely few and small).

As demands on water resources increase, our data can help address the ecological risks associated with further impacts on LRSs. For example, in free-flowing rivers, biodiversity can persist because organism dispersal can be effective in both upstream and downstream directions (*40*, *41*) and because many organisms are likely to adapt to climate change by concomitant shifts in distributions. But in fragmented and regulated rivers, such dispersal can be strongly limited (*10*). These facts need to be accounted for in global planning for sustainable river management.

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24. Following (*23, 25*), we synthesized our data on channel fragmentation and flow regulation to classify the river systems as strongly affected, moderately affected, or not affected (table S2). When reclassifying the northern 139 LRSs, we updated data on dams and excluded previously reported data on irrigation consumption. We excluded previously assessed irrigation data because a global, more consistent data set became available, which we analyzed for all 292 LRSs. We did, however, continue to consider data on interbasin diversions when reclassifying the northern LRSs, because no global and consistent data were available for analysis. Data on interbasin diversions for the 153 nonnorthern LRSs were largely unavailable and thus not considered during impact classification for those systems.
25. Information on materials and methods is available on *Science* Online.
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29. We calculated flow regulation as the sum of reservoir capacity within a river system [see (*25*) for data sources] and expressed this measure as the percentage of the LRS's volumetric annual discharge that can be contained and released by the reservoirs (live storage). One-half of the gross capacity was used as a substitute for live storage for reservoirs that lacked live storage data. The gross capacity is the total water volume that can be retained by a dam, including the bottom water that cannot be released through the lowest outlet. Live storage is the gross capacity excluding this bottom water.
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36. We considered the minimum 2003 per-capita GDP of OECD member nations (*46*) as a cutoff between weak and strong economies. An LRS's economy was considered strong if its GLP (calculated per capita in this case, rather than per discharge) was greater than or equal to the cutoff. LRSs with GLPs lower than the cutoff were considered to have weak economies. (Mexico's per-capita GDP of $9300, second to lowest among all OECD member nations, was selected as the cutoff. Turkey represented the actual minimum, but data used to calculate Turkey's per-capita GDP were inconsistent with those used for the other OECD member nations; thus Turkey was excluded from selection.)
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46. More information is available online at www.OECD.org.
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Materials and Methods
Tables S1 and S2

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Crystal Structure of the Malaria Vaccine Candidate Apical Membrane Antigen 1

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Apical membrane antigen 1 from *Plasmodium* is a leading malaria vaccine candidate. The protein is essential for host-cell invasion, but its molecular function is unknown. The crystal structure of the three domains comprising the ectoplasmic region of the antigen from *P. vivax*, solved at 1.8 angstrom resolution, shows that domains I and II belong to the PAN motif, which defines a superfamily of protein folds implicated in receptor binding. We also mapped the epitope of an invasion-inhibitory monoclonal antibody specific for the *P. falciparum* ortholog and modeled this to the structure. The location of the epitope and current knowledge on structure-function correlations for PAN domains together suggest a receptor-binding role during invasion in which domain II plays a critical part. These results are likely to aid vaccine and drug design.

Apical membrane antigen 1 (AMA1) is currently in clinical trials as a vaccine against *P. falciparum*, the species causing the most serious forms of malaria in humans. AMA1 is present in all *Plasmodium* species examined (*1*), and orthologs exist in other *Apicomplexa*, including *Toxoplasma* (*2*) and *Babesia* (*3*). Although little is known about its molecular function, genetic evidence indicates a role in maintaining parasite growth during the blood-stage cycle (*4*). Antibodies raised against AMA1 can inhibit erythrocyte invasion and protect against the disease in animal-model systems of malaria (*5–9*). Furthermore, invasion-inhibitory antibodies to AMA1 have been affinity-purified from human sera of donors from malaria-endemic regions (*10*). AMA1 is stored in the microneme organelles after synthesis and is translocated to the parasite surface just before or