Homogenization of regional river dynamics by dams and global biodiversity implications

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Global biodiversity in river and riparian ecosystems is generated and maintained by geographic variation in stream processes and fluvial disturbance regimes, which largely reflect regional differences in climate and geology. Extensive construction of dams by humans has greatly dampened the seasonal and interannual streamflow variability of rivers, thereby altering natural dynamics in ecologically important flows on continental to global scales. The cumulative effects of modification to regional-scale environmental templates caused by dams is largely unexplored but of critical conservation importance. Here, we use 186 long-term streamflow records on intermediate-sized rivers across the continental United States to show that dams have homogenized the flow regimes on third- through seventh-order rivers in 16 historically distinctive hydrologic regions over the course of the 20th century. This regional homogenization occurs chiefly through modification of the magnitude and timing of ecologically critical high and low flows. For 317 undammed reference rivers, no evidence for homogenization was found, despite documented changes in regional precipitation over this period. With an estimated average density of one dam every 48 km of third- through seventh-order river channel in the United States, dams arguably have a continental scale effect of homogenizing regionally distinct environmental templates, thereby creating conditions that favor the spread of cosmopolitan, nonindigenous species at the expense of locally adapted native biota. Quantitative analyses such as ours provide the basis for conservation and management actions aimed at restoring and maintaining native biodiversity and ecosystem function and resilience for regionally distinct ecosystems at continental to global scales.

disturbance | natural flow regime | ecosystem sustainability | environmental template

R egional-scale variation in climate is a key driver of global biodiversity (1, 2), in large part through its effects on dynamic natural disturbance regimes that shape evolutionary and ecological processes in aquatic and terrestrial ecosystems. In recent times, however, human transformation of the biosphere is not only threatening the biodiversity of ecosystems worldwide (1, 3), but may also be overriding important regional-scale differences in natural climatic variation that shape the bounds of ecosystem resilience. Humans have certainly simplified natural landscapes through extensive ecosystem modification and domination (4), but a fundamental question remains as to whether humans are diminishing, or homogenizing, the regional distinctiveness in natural disturbance dynamics, as some have speculated based on documented large-scale patterns of biotic homogenization (5, 6). If so, an immediate concern would be identifying possible conservation strategies to maintain or restore ecologically important regional differences to support ecosystem resilience and biodiversity at continental to global scales.

The construction and operation of >45,000 large (>15 m high) dams worldwide during the 20th century (7) has severely altered the global flux of water and sediment from continents to oceans through the world's river basins (8, 9). From an ecological perspective, the fragmentation of river corridors by dams (10) and the associated modification of fluvial processes and streamflow dynamics pose significant threats to native river biodiversity on a global scale (11–14). The numerous negative effects of individual dams on individual river ecosystems are well documented (15–17); however, an important, unresolved question is whether the cumulative effects of dams are inducing continental to global scale convergence of historically distinctive regional environmental templates, thereby diminishing regional-scale variation that helps maintain broader patterns of native biodiversity (18). This question can be addressed quantitatively for the United States because long-term, spatially extensive, and high-quality daily streamflow records exist that allow natural disturbance regimes to be characterized in an ecologically meaningful manner.

A broad consensus has emerged over the last 10 years among ecologists that the function of riverine ecosystems, and the evolutionary adaptations of resident biota, are often dictated by the dynamic nature of a river's natural disturbance regime, which largely reflects time-varying streamflow conditions (12, 13, 19, 20) that vary from region to region (21, 22). By strongly modifying natural flow regimes, dams have the potential to reduce these natural regional differences and thus impose environmental homogeneity across broad geographic scales. Many techniques have been developed to characterize the statistical properties of a river's flow regime for ecological study (23, 24), and the occurrence of long-term, daily hydrographic records allows regional-scale analysis of ecologically relevant streamflow modification by dams on the nation's rivers. Likewise, ongoing monitoring of free-flowing rivers allows the effects of river regulation on regional disturbance regimes to be distinguished from the natural range of variation associated with climate-driven changes in regional precipitation and river runoff that have occurred over the 20th century (25, 26).

Here, we quantitatively test the hypothesis that dams have homogenized regionally distinct river flow regimes across the
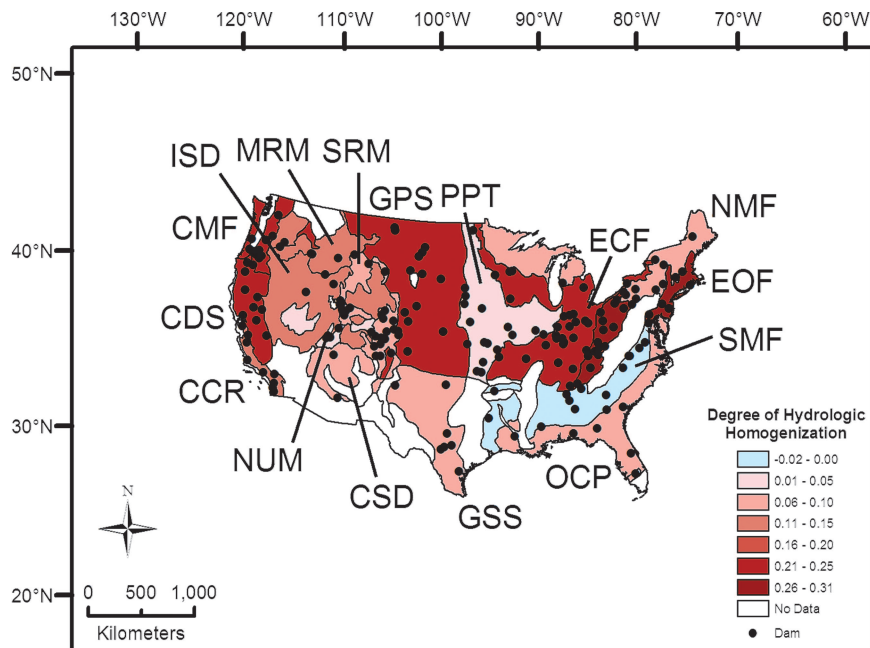

Fig. 1. Hydroregion map and dam locations (dots) used in analysis for the continental United States. Shading of the individual regions refers to degree of regional homogenization in flow regimes in the postdam period (see Fig. 3). White regions were excluded because of inadequate dam-gauge pairs.

continental United States, independently of climatic variation. Over the course of the 20th century, >75,000 structures exceeding 2 m in height were constructed on stream and river channels in the United States (ref. 27; http://crunch.tec.army.mil/nid/webpages/nid.cfm). These ubiquitous dams occur on average about every 70 km on the ≈5.2 million km of river channels ranging from first-order small streams to 10th-order great rivers (28). The effects of these dams extend both upstream by inundating ≈10% of the total stream and river channel length (29) and downstream by modifying flow regimes and other environmental factors for tens to hundreds of km (15, 30). Indeed, unregulated, free-flowing rivers are now rare in the United States, with only 42 rivers >200 km being free from the influence of dams (31).

In this article, we focus on third- through seventh-order rivers, which comprise over a quarter of the total stream channel kilometers in the U.S (28). Using river disturbance theory (12, 32), we define flow regimes in terms of magnitude, frequency, duration, and timing of ecologically relevant flows, expressed both as long-term averages and interannual variation. For 16 *a priori* defined "hydroregions" across the continental U.S., we use a total of 186 long-term, daily streamflow gauges to calculate each region's predam, unregulated flow regime and postdam, regulated flow regime (Fig. 1). In these same regions, we use 317 undammed reference gauges that allow quantitative comparison of the magnitude of changes in regional flow regimes caused by dams versus climatic variation over the same time period.

Results and Discussion

Regional-scale differences in natural flow regimes that existed in the first half of the 20th century in the United States have been significantly reduced in regulated rivers, but not in free-flowing rivers. Across the 16 regions, postdam homogenization is statistically significant [analysis of similarity (ANOSIM) global $\bar{\Delta}R = 0.13$, range −0.02 to 0.31; one-sided t test: $t_{15} = 5.40$, $P < 0.0001$; Fig. 2A]. In contrast, undammed reference rivers show no evidence for flow homogenization over the same period (ANOSIM global $\bar{\Delta}R = -0.003$, range −0.17 to 0.08; $t_{15} = -0.17$, $P = 0.44$; Fig. 2B). Because regulated and reference rivers

within regions have presumably experienced similar climate conditions and trends, we conclude that this homogenization is caused by the effects of dams and not by changes in regional climate over this period (25, 26). Evidence for dam-induced flow homogenization is further supported by the significant difference between regulated and unregulated rivers for each region (paired t test: $t_{15} = 5.34$; $P < 0.0001$).

Overall, 15 of the 16 regions show evidence of flow homogenization (Fig. 1). Those regions showing the greatest average increase in similarity ($\bar{\Delta}R$ values) also show the highest frequency of pairwise interregional homogenization (ΔR values in Fig. 3) before and after damming. Overall, for regulated rivers, a total of 88 (73%) of the 120 pairwise comparisons among the 16 regions exhibited flow homogenization (i.e., positive ΔR values), which was significantly more than the 60 (50%) for reference rivers (sign test: $P < 0.001$).

Different characteristics of the flow regime (depicted by the 16 flow metrics) have been affected by dams, and thus differentially contribute to observed levels of flow homogenization among regions (Fig. 4). Broadly speaking, operations of the dams examined tend to homogenize regional flow variability by modifying the magnitude and timing components of high and low flows, with lesser contributions from changes in flow duration and frequency. Across almost all regions, average maximum flow consistently declined, as did interannual variation in daily maxima. Minimum flow magnitudes generally increased, whereas interannual variation in minimum flows generally declined. Timing of maximum flows exhibited a geographic pattern, with more eastern, rainfall-dominated regions showing earlier timing of peak flows [e.g., Eastern Broadleaf Forest–Oceanic (EOF), Eastern Broadleaf Forest–Continental (ECF), and Southeastern Mixed Forest (SMF)] compared with delayed peak flows in more snowmelt-dominated western regions [e.g., California Dry Steppe (CDS), Cascade Mixed Forest-Coniferous Forest-Alpine Meadow (CMF), and Middle Rocky Mountain Steppe-Coniferous Forest-Alpine Meadow (MRM)]. Trends in the timing of minimum flows were more variable. The interannual variation in timing for both maximum and minimum flows
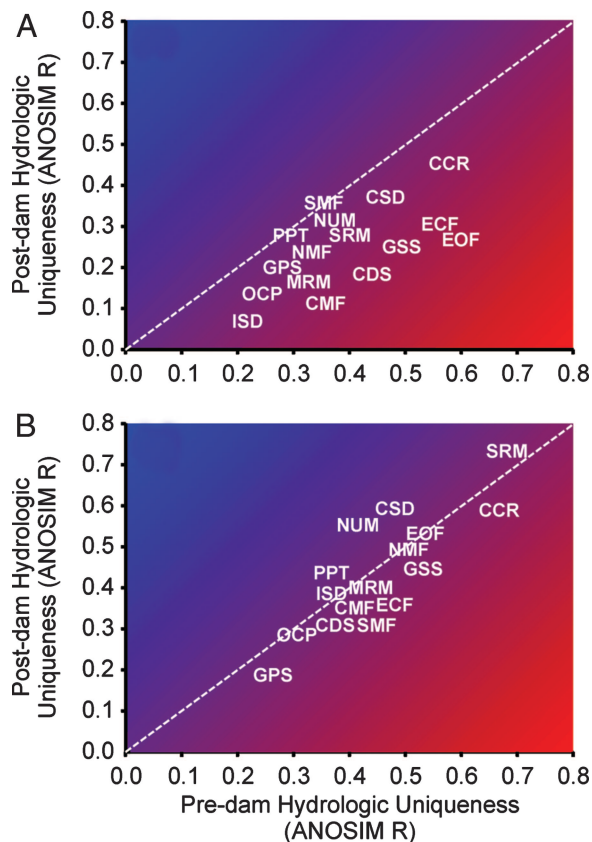
Fig. 2. Changes in flow regime similarity for 16 regions over the course of the 20th century. (*A*) Data for 186 dammed rivers. (*B*) Data for 317 unregulated, reference rivers. *x* axis scores represent a region's hydrologic uniqueness before regulation (mean predam $\bar{\Delta}R$), and *y* axis scores are postdam uniqueness (mean postdam $\bar{\Delta}R$). The 1:1 dotted line is the expected relationship between predam and postdam flow regimes for the null hypothesis of no change over time. Regions plotting below this line have become less distinct in the postdam period (homogenization) and those above have become more distinct (differentiation) relative to other regions. See *Methods* for assignment of reference rivers to predam and postdam periods.

generally increased across regions irrespective of geography and climate.

Because regions differ in their natural (predam) patterns of river runoff, increased flow similarity among specific regions caused by dams can result from a diverse set of modifications to natural flow regimes in different regions. This is best illustrated for the regions EOF and Great Plains Steppe and Shrub (GSS), which are among the most homogenized by dams and show strong pairwise flow convergence ($\Delta R > 0.40$) with five other geographically disjunct regions (Fig. 3). For the eastern region, EOF, the specific flow changes relative to the differential flow alterations in other, now-similar regions (Fig. 4), indicate that western regions [Intermountain Semidesert (ISD), California Coastal Range Open Woodland-Shrub-Coniferous Forest-Meadow (CCR), and MRM] converged via reductions in minimum flow variation and delayed timing of maximum flows. MRM, a seasonal snowmelt region, also became more variable in peak flow timing and less variable in minimum flow timing. By contrast, an eastern region [Outer Coastal Plain Mixed Forest (OCP)] converged in part through an increase in minimum flow variation and a decrease in peak flow variation. The midwestern region (GSS) lost variation in interannual peak flow magnitude and now has later minimum flows. The five regions converging with the midwestern region, GSS, included three western regions: Intermountain Semidesert (ISD), which became more

similar via reduction in minimum flows, and CDS and CMF, which converged via delayed timing and a reduced interannual variation in peak flows. Two eastern regions, EOF and ECF, became more similar via reduced minimum flows, earlier peak flows, and earlier minimum flows.

These results illustrate how a broad range of hydrologic alterations caused by dams can induce flow homogenization across geographically disjunct regions, often in an idiosyncratic manner. Indeed, neighboring regions may be less likely to become homogenized, given their relatively similar climates and potentially similar dam management strategies. For example, the two regions with the highest mean $\bar{\Delta}R$ showed little interregional homogenization (EOF and ECF; Fig. 3), which reflects their relative hydrologic similarity in the predam and postdam periods (Figs. 2*A* and 4).

Our results also suggest that the cumulative effects of river regulation across the U.S. in the 20th century mask (and even counter) the natural, climate-driven variation in flow regimes on regulated rivers. Interestingly, dams have a general homogenizing effect, irrespective of specific dam attributes that can differentially affect flow regimes. For example, both dam height or storage capacity and operational mode (e.g., hydropower peaking) strongly influence downstream hydrographs (16). Statistical stratification on these factors was infeasible given our sample size; however, there was no significant correlation ($P > 0.3$) between degree of regional homogenization and average values for these dam attributes, or other factors including basin size and regional annual precipitation.

Based on our analysis, we argue that dams are homogenizing natural flow regimes for entire regions across the U.S., even though data availability restricted our analysis to 186 regulated river hydrographs. We estimate there is, on average, one dam every 48 km of third- to seventh-order river channel in the U.S. (see *Methods*). The downstream effects of individual dams on river hydrology typically extend for tens to hundreds of kilometers (14, 15, 30). In our analysis we cannot determine the spatial extent of flow alteration for the 186 dams; however, we note that the median distance between a dam and the downstream stream gauge was 12 km (mean = 17 km). If downstream flow alterations extend, conservatively, only twice the median downstream gauge distance (i.e., 24 km), up to 50% of all third- to seventh-order river channel length could be affected. We also note that, although outside the domain of this study, dams occur on average every 80 km on small first- to second-order streams and every 100 km on very large eighth- to 10th-order rivers, further indicating the potential for dams to impose continental-scale flow homogenization.

We also hypothesize that dams are contributing to global-scale homogenization of fluvial dynamics across broad climatic regions known to have distinctive runoff patterns (21, 22). Outside of North and Central America there are some 40,000 so-called large dams (>15 m high) (7), and innumerable undocumented smaller structures impound small rivers worldwide. Unfortunately, adequate streamflow data are not available for a quantitative analysis at this time.

Our findings have broad-scale ecological implications that are directly applicable to management and conservation of aquatic and riparian ecosystems. Dam-induced flow changes alone are known to alter ecological diversity and function on individual rivers (12, 13), where they often act synergistically with other dam-induced alterations, including disruption of sediment flux (8, 15), geomorphic simplification (17), floodplain disconnection (12, 16), thermal regime alteration (15), and extensive longitudinal and lateral fragmentation of river corridors (10).

The ecological consequences of regional hydrologic alteration are poorly understood, but important (18). Indeed, biotic homogenization of freshwater fish faunas in the U.S. (33) has been hypothesized to be facilitated by broad-scale river regulation,

	EOF	ECF	CDS	CMF	GSS	ISD	MRM	CCR	OCP	GPS	SRM	NMF	CSD	NUM	PPT	SMF	Mean $\overline{\Delta R}$
EOF		0.06	-0.06	-0.06	0.04	-0.11	0.10	0.02	0.06	0.03	-0.01	-0.01	-0.02	-0.14	-0.09	-0.03	-0.01
ECF	0.19		0.07	0.08	0.15	0.11	0.34	0.14	0.12	0.13	0.07	0.04	0.02	-0.13	0.04	0.00	0.08
CDS	0.29	0.25		-0.10	0.16	-0.05	0.08	0.21	0.07	0.11	-0.04	-0.04	0.07	-0.03	-0.13	0.11	0.03
CMF	0.20	0.17	0.18		0.14	-0.06	0.23	0.09	0.01	0.09	-0.05	-0.05	0.13	-0.23	-0.09	0.12	0.06
GSS	0.55	0.45	0.52	0.49		0.09	0.16	0.11	-0.01	0.03	-0.03	0.01	-0.18	0.10	-0.03	0.18	0.02
ISD	0.46	0.41	0.31	0.34	0.43		0.23	0.05	-0.01	0.08	-0.11	-0.01	-0.13	-0.27	-0.03	0.12	-0.01
MRM	0.45	0.23	0.33	0.21	0.34	0.11		-0.03	0.15	0.20	-0.45	0.14	-0.34	-0.55	0.17	0.32	-0.01
CCR	0.41	0.29	0.25	0.49	0.04	-0.06	-0.01		0.16	0.20	-0.06	0.00	-0.16	-0.01	-0.11	0.21	0.03
OCP	0.52	0.42	0.32	0.31	0.07	0.01	-0.10	-0.05		-0.01	-0.05	0.03	-0.32	-0.09	-0.11	0.07	0.05
GPS	0.31	0.27	0.13	0.21	-0.14	0.08	-0.15	0.14	0.13		0.02	0.04	-0.06	0.10	-0.06	0.09	0.07
SRM	0.07	0.12	0.00	-0.05	0.06	0.22	-0.07	0.16	0.23	0.14		-0.06	-0.08	-0.04	-0.15	0.04	0.00
NMF	0.13	0.14	0.12	0.07	0.14	0.18	0.07	0.11	0.21	0.13	0.09		-0.10	-0.23	0.01	0.00	-0.07
CSD	0.30	0.20	0.49	0.17	0.21	-0.29	0.39	-0.31	-0.34	0.20	0.22	-0.08		-0.68	-0.22	0.09	-0.02
NUM	0.25	0.09	0.35	0.41	0.03	-0.05	0.14	-0.04	-0.39	-0.03	0.12	-0.05	0.18		-0.33	-0.03	-0.13
PPT	0.27	0.20	0.04	0.14	0.04	0.03	-0.11	0.05	0.04	-0.16	-0.05	-0.03	-0.11	-0.13		-0.09	-0.17
SMF	0.24	0.28	-0.09	0.01	0.06	-0.06	-0.22	0.04	0.02	0.02	-0.02	-0.05	-0.19	-0.26	-0.04		0.08
Mean $\overline{\Delta R}$	0.31	0.25	0.23	0.22	0.22	0.14	0.11	0.10	0.09	0.09	0.08	0.08	0.07	0.04	-0.02	0.01	

Fig. 3. Results from the ANOSIM showing all pairwise differences between the 16 hydroregions for the predam vs. postdam flow regimes. Each cell represents a specific pairwise comparison, with colored shading representing the degree of homogenization. Increasing intensity of red indicates greater positive values of ΔR (i.e., interregional flow homogenization), white shading indicates $\Delta R = 0$, and increasing intensity of blue indicates greater negative values ΔR (i.e., interregional flow differentiation). The black diagonal separates the pairwise comparisons for the regulated rivers (below diagonal) to those for unregulated, reference rivers (above diagonal). The average of the 15 pairwise comparisons for each regions is the average regional homogenization score for that region ($\overline{\Delta R}$), as plotted in Fig. 1. The $\overline{\Delta R}$s for the regulated rivers are given across the bottom row and for the reference rivers in the right-most column (e.g., EOF regulated $\overline{\Delta R} = 0.31$ and EOF unregulated $\overline{\Delta R} = -0.01$). Visual inspection reveals that inter-regional homogenization is greater for regulated rivers (lower matrix, average $\overline{\Delta R} = 0.13$) than unregulated rivers (upper matrix, average $\overline{\Delta R} = 0.00$).

which presumably simplifies regionally unique disturbance dynamics and allows establishment of nonnative and otherwise poorly adapted species (34, 35). As humans continue to face the dilemma of attaining ecosystem sustainability in the face of global change (1, 36), there is growing need for preservation of remaining intact systems and deliberate and strategic design of resilient ecosystems (37). Therefore, for rivers, and other ecosystems, maintaining dynamic elements of regional distinctiveness in key environmental drivers of ecosystem function and native biodiversity should be a conservation priority, as this will contribute landscape-scale ecosystem resilience in the face of global change (1, 4, 38). Opportunities such as dam re-regulation to provide formative flows having some semblance to the historical regime should be exploited (39–41), as should the conservation potential of relatively free-flowing rivers that can serve as cornerstones of "dynamic reserves" (42, 43) in an increasingly homogenized world.

Methods

Delineation of Hydrologic Regions. We developed our *a priori* hydroregions by modifying an existing ecoregional classification (44) comprised of 19 divisions and 35 provinces, which adequately partition the climatic and geologic variability of the continental U.S. at the national scale. We split some divisions that spanned wide latitude or elevation gradients along province boundaries and by clumping some divisions with provinces belonging to other divisions. This pseudodivision scheme partitions the hydrologic variability of the continental U.S. in a manner we deemed to be more ecologically meaningful than that afforded by other mapping schemes based on hydroclimatology (45), climate and vegetation (46), or point distribution of streamflow "types" (47).

We selected final regions based on criteria of adequate stream gauge density (see below). The 16 regions we used (Fig. 1) were: Adirondack-New England Mixed Forest-Coniferous Forest-Alpine Meadow (NMF), CCR, CDS, CMF, Colorado Plateau Semidesert (CSD), ECF, EOF, GSS, Great Plains Steppe (GPS), ISD, MRM, Nevada-Utah Mountains-SemiDesert-Coniferous Forest-Alpine Meadow (NUM), OCP, Prairie Parkland–Temperate (PPT), SMF, and Southern Rocky Mountain Steppe-Open Woodland-Coniferous Forest-Alpine Meadow (SRM).

Selection of Long-Term Streamflow Gauges. In identifying suitable dam-gauge pairs to assess hydrologic alteration by dams, we first identified all 26,000 streamflow gauges contained in the Environmental Protection Agency BASINS V 3.0 database (48), including those no longer active. These were geo-referenced (latitude-longitude) in a Geographic Information System on a river reach coverage (RF1) at a scale of 1:250,000, which captures ≈1.12 million km of river channels and open waters in the continental U.S. Based on stream length to stream order relations, the minimum scale of this coverage is about a third-order river (28). We extracted information from the U.S. National Inventory of Dams (NID; ref. 27; http://crunch.tec.army.mil/nid/webpages/nid.cfm), which contains >75,000 structures >2 m in height. Next, we identified those dams on RF1 segments (using a 0.8-km buffer to remove off-channel reservoirs). We restricted our analysis to those dams that had a designated
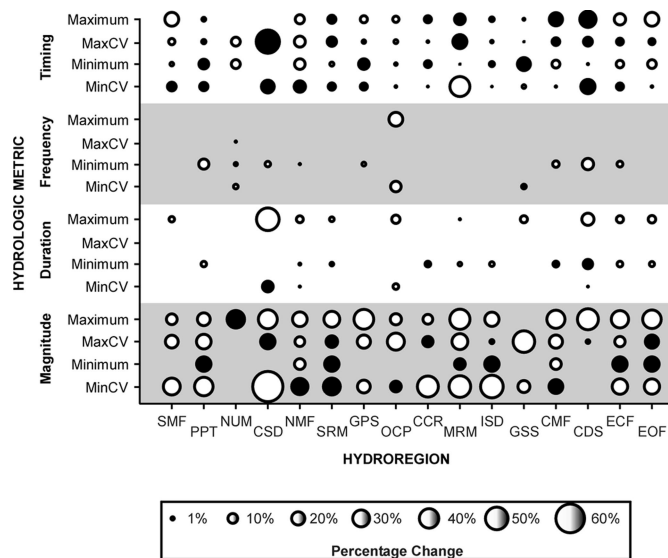
Fig. 4. Relative contributions of 16 hydrologic metrics to flow homogenization for dammed rivers in 16 hydroregions. Metrics include magnitude, duration, frequency, and timing for average high flows and low flows and their interannual coefficient of variation (CV). For each region, the size of the circle represents the percent change in the relative importance of the metric for describing interregional flow difference from predam to postdam periods. Filled symbols indicate an increase in the magnitude of the metric from predam to postdam period for each region, and unfilled symbols indicate a decrease. Regions are ordered from left to right according to the increasing degree of homogenization (i.e., based on the mean $\bar{\Delta}R$).

primary operational purpose of irrigation, hydropower, flood control, navigation, water supply, or recreation, but these NID categories are not mutually exclusive in terms of potential downstream hydrologic impacts and are qualitative.

Of the ≈17,000 dams in our reduced candidate set, we used the following strict criteria to ensure accurate recording of the effect of a single dam on the flow history of the river gauge: no preexisting upstream mainstem dam, at least 15 years of daily streamflow data both before and after the dam completion date, no more than two tributary inputs between the upstream dam and the gauge, and no dams on tributaries with an estimated drainage area larger than the mainstem river of the candidate dam. Flow gauges on dammed rivers were located 0.1–74 km downstream of dams (mean = 17 km, median = 12 km). Only regions with at least two gauges were included, for a total of 186 gauges on currently regulated rivers in 16 regions (Fig. 1). For these gauges there were, on average, 32 years of predam daily flow data and 33 years of postdam data. All streamflow data were obtained from the U.S. Geological Survey National Water Information System (ref. 49; http://waterdata.usgs.gov/nwis).

For the same regions, 317 reference (undammed) rivers were selected from the U.S. Geological Survey's sentinel gauge network. These gauges, which include most of the Hydroclimatic Data Network gauges (50), are relatively unaffected by flow regulation and characterize major ecoregions and river basins (ref. 51; http://water.usgs.gov/nsip/federalgoals.html); therefore, discharge records from these gauges can be used to describe hydrologic changes caused by factors other than flow regulation, e.g., climate change.

Drainage area ranged from 57 to 723,902 km² (median = 1,202 km²) for dammed rivers and from 19 to 16,757 km² (median = 627 km²) for reference rivers. For the 186 dammed river, 3% of basins ranged from 27 to 131 km² (about third order; ref. 28), 29% from 132 to 620 km² (about fourth order), 37% from 621 to 2,946 km² (about fifth order), 18% from 2,947 to 13,993 km²

(about sixth order), and 13% from 13,994 to 66,552 km² (about seventh order, with six of these from arid lands having drainage areas estimated in the eighth-order range). For these same ranges of drainage areas for the 317 reference rivers, the percentages were 7%, 42%, 42%, 9%, and 1%, respectively.

To compare changes in flow regimes for reference versus regulated rivers over comparable time periods, we divided the flow records for each of the reference rivers into two time series that corresponded to the free-flowing and regulated periods for the dammed rivers. Specifically, for each reference river in each region, we calculated a predam and postdam flow record based on the dam construction dates for each of the regulated rivers in that region. Thus, each reference river had as many replicate predam vs. postdam simulations as there were dammed rivers in the region (median = 9). We then averaged the replicated predam and postdam hydrologic variables for each river to generate that river's predam and postdam flow regime. On average, the reference gauges had 32 years of predam and 31 years of postdam daily streamflow data.

There are ≈8.4 × 10⁶ km of stream and river channels in the continental U.S. (28). Of this total, small streams (first–second order) comprise 73% of total distance, intermediate rivers (third–seventh order) 26.5%, and large to very large rivers (eighth–10th order) 0.5%. In the National Inventory of Dams only 39% of dams report drainage areas, and of these 37% are in the range associated with third- to seventh-order rivers. Applying this fraction to all dams in the database, we estimate ≈28,500 dams occur on these third- to seventh-order river channels nationwide, for an average of one dam every 48 km. In our analysis, we excluded small streams because suitable streamflow records are relatively sparse and streams of this size could not be resolved with our river reach Geographic Information System coverage. We also removed large to very large rivers because they are typically influenced by multiple upstream dams and thus lack adequate predam flow records.

Definition of Flow Regimes. We defined the natural flow regime of a river in terms of the magnitude, frequency, duration, and timing of extreme high flows and low flows. These four flow components comprise a regime of hydrologic disturbance, and together they generate much of the temporal variation that maintains ecological and evolutionary distinctiveness within and among rivers (12, 13, 20). Specifically, we defined 16 hydrologic metrics to characterize the variable flow regime for each river: two flow classes (high and low) × four components × two time scales (long-term mean and interannual variation), which were calculated separately for the predam and postdam periods. High flows were defined as the average maximum annual 24-h discharge (magnitude), the number of times per year that the 24-h daily flow exceeds the average 1-day predam (natural) maximum (frequency), the number of days per year the mean average maximum predam flow is exceeded (duration), and the average Julian date of the annual maximum flow (timing). For each of these four variables the interannual coefficient of variation was also calculated. The same procedures were used to develop the low flow metrics, except that the threshold quantity was based on the average annual 7-day low flow.

Statistical Analysis. We used an ANOSIM based on the Bray-Curtis dissimilarity coefficient (52) to test the null hypothesis of no difference in flow regimes (according to the 16 flow metrics) among all 16 regions using PRIMER version 5.2.9 software (53). By comparing the regional-scale differences in flow regimes in the period before versus after damming, it is possible to assess the degree to which dams have diminished, or homogenized, regional-scale differences in flow regimes over the course of the 20th century.

ANOSIM tests for differences in rank dissimilarity between *a*

priori-defined groups (here, rivers in hydroregions) compared with randomly assigned groups. The ANOSIM statistic R, which is based on the difference in the mean ranks between hydroregions and within hydroregions, is scaled from -1 to $+1$ and describes the hydrologic uniqueness for each region. A value of 1 indicates that all rivers within a region are more similar to one another than to any rivers from different regions; a value of 0 indicates that there is no difference among rivers across regions; and, a value of -1 indicates that all rivers within regions are less similar to one another than any rivers from different regions (54). ANOSIM is particularly suited for this analysis as it can explicitly test for differences in flow regime characteristics between hydroregions based on an interpretable statistic that measures how dissimilar regions are. Further, because ANOSIM compares rank to random comparisons, it is robust against inflated probability of significance given multiple comparisons (Fig. 3) and to differences in sample size (i.e., between dammed and reference rivers) (54).

A value of R was calculated for each region for the predam and postdam periods. This was done separately for the 186 regulated rivers and the 317 free-flowing rivers. The difference in R between any two regions before dams and after dams, ΔR, is a measure of how dams have changed the similarity of flow regimes for those specific regions. A positive ΔR indicates increased flow similarity among the two regions (i.e., homogenization), whereas a negative ΔR indicates decreased flow similarity among the two regions. For our data set there are 120 such pairwise comparisons of regional changes in flow regimes associated with damming. Likewise, there are 120 pairwise comparisons for the predam and postdam periods for the reference gauges.

To test the hypothesis of continental–scale homogenization of flow regimes, we first calculated the average of the 15 pairwise ΔR values for each region (designated as $\overline{\Delta R}$). Second, we used a one-tailed Student's t test to evaluate whether the global $\overline{\Delta R}$ (i.e., average across all 16 regional $\overline{\Delta R}$s) was both positive (i.e., >0 indicating continental-scale homogenization) and greater than that measured for the reference, unregulated rivers.

To quantify the relative contributions of the 16 hydrologic metrics to observed patterns of flow homogenization among regions, we used the SIMPER procedure in PRIMER. For both the predam and postdam periods, we calculated the relative contributions of the individual metrics for explaining the observed difference between each hydroregion and all other regions. Percent change in the relative contributions from predam to postdam years was calculated. Values >0 indicate those metrics whose importance in distinguishing a particular region from all others in the postdam years declined relative to its importance in the predam years, i.e. they contribute the most to flow homogenization.

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