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How Does Flow Alteration Propagate Across a Large, Highly Regulated Basin? Dam Attributes, Network Context, and Implications for Biodiversity

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Key Points:

- Dams cumulatively altered streamflow in the Colorado River Basin. Tributaries did not re-set natural flow variation in the lower main stem
- Dam-induced flow alteration was driven by spatial context (location, upstream regulation) more than by local dam properties (e.g., storage)
- Basin-wide reoperation should be considered in efforts to mitigate flow alteration and associated biodiversity impacts

Supporting Information:

Supporting Information may be found in the online version of this article.

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How Does Flow Alteration Propagate Across a Large, Highly Regulated Basin? Dam Attributes, Network Context, and Implications for Biodiversity

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Abstract Large dams are a leading cause of river ecosystem degradation. Although dams have cumulative effects as water flows downstream in a river network, most flow alteration research has focused on local impacts of single dams. Here we examined the highly regulated Colorado River Basin (CRB) to understand how flow alteration propagates in river networks, as influenced by the location and characteristics of dams as well as the structure of the river network—including the presence of tributaries. We used a spatial Markov network model informed by 117 upstream-downstream pairs of monthly flow series (2003–2017) to estimate flow alteration from 84 intermediate-to-large dams representing >83% of the total storage in the CRB. Using Least Absolute Shrinkage and Selection Operator regression, we then investigated how flow alteration was influenced by local dam properties (e.g., purpose, storage capacity) and network-level attributes (e.g., position, upstream cumulative storage). Flow alteration was highly variable across the network, but tended to accumulate downstream and remained high in the main stem. Dam impacts were explained by network-level attributes (63%) more than by local dam properties (37%), underscoring the need to consider network context when assessing dam impacts. High-impact dams were often located in sub-watersheds with high levels of native fish biodiversity, fish imperilment, or species requiring seasonal flows that are no longer present. These three biodiversity dimensions, as well as the amount of dam-free downstream habitat, indicate potential to restore river ecosystems via controlled flow releases. Our methods are transferrable and could guide screening for dam reoperation in other highly regulated basins.

Plain Language Summary Despite long-standing efforts to reduce impacts of dams on river biodiversity and ecosystem processes, our understanding of how altered flow regimes propagate in river networks is incomplete. Here we used the Colorado River Basin as a model system to examine how dams alter flow regimes, both individually and cumulatively, as water flows downstream a river network. We found that impacts accumulated downstream, and tributaries were unable to reset natural flow variation in the lower main stem. Although local dam properties (e.g., storage) were important in determining how impactful individual dams were, spatial context (location in the network and upstream regulation) was paramount. Our results advance the notion that basin-wide reoperation should be considered in any effort to mitigate flow alteration—a critical need in light of new damming in developing economies.

1. Introduction

Dams are a major contributor to flow regime alteration: they increase water residence time, mute peak flows, shift the timing of ecologically important high and low flows, and alter flow periodicity (Poff et al., 2007; Ruhi et al., 2018; Vorosmarty, 1997). These alterations adversely affect riverine and riparian biodiversity because the life-history, morphological, and behavioral adaptations of organisms are often at odds with the novel environmental regime (Bunn & Arthington, 2002; Lytle & Poff, 2004; Mims & Olden, 2013). Such flow regime alteration is also often detrimental to society, as it may disrupt floodplain fishing, flood-recession agriculture, and a wide range of recreational and cultural values (Anderson et al., 2019). Despite intense scrutiny, flow alteration by dams has largely been estimated via methods that do not take into account the spatial context in which these changes

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are occurring (Richter et al., 1998; Singer, 2007). This view assumes that dams have location-invariant, additive impacts within a river basin; and that free-flowing tributaries have minimal effects on the regulated main stems they join. However, significant evidence challenges both assumptions: flow regimes and flow-dependent ecosystem processes are strongly influenced by river network topology, and inferences can vary based on the location of the study reach within the river network (Brown & Swan, 2010; Campbell Grant et al., 2007; Henriques-Silva et al., 2019). Leveraging network context-dependencies, instead of ignoring them, could be an important step toward informing river ecosystem restoration via dam operation. This shift could also be important for prioritizing dam decommissioning (Guetz et al., 2021), or for mitigating socio-environmental impacts in global regions where dam construction is underway (Flecker et al., 2022; Holtgrieve & Arias, 2022).

River network structure, and the spatial distribution of dams and their attributes (e.g., size and purpose), may influence how flow regime alteration is propagated across the river network. For instance, different types of dams and their operation schedules generally co-occur in a basin, altering hydrographs in cumulative ways as water flows downstream. Downstream dams can "inherit" particular aspects of upstream flow alteration—or swamp them if local storage relative to runoff is large enough (Holt et al., 2015; Singer, 2007). In turn, free-flowing tributaries could partially restore main-stem flow regimes, benefitting ecological communities by reestablishing certain aspects of flow variability (e.g., seasonal pulse flows) and by physically connecting habitats between regulated river sections and unfragmented watersheds (Katano et al., 2009; Sabo et al., 2018; Ward & Stanford, 1995). The importance of river confluences has been long recognized in river ecology (Poole, 2002), but their contributions in the context of serial discontinuity created by dam cascades remain to be fully analyzed (Sabo et al., 2018). Large, highly regulated basins offer an opportunity to study how flow alteration propagates across a dendritic network, and to disentangle the effects of local versus network-level factors on flow regime alteration.

Abundant research around the natural flow regime concept (Poff et al., 1997) has explored the link between the different facets of flow regime (i.e., magnitude, frequency, duration, and timing of high- and low-flow events) and the provision of ecological outcomes (e.g., persistence of native freshwater biodiversity). In turn, these relationships have led to the development of the *Ecological Limits of Hydrologic Alteration* framework, and associated design of environmental flows (Poff, 2018; Poff et al., 2010). Higher-order properties of a flow regime, such as its seasonality and interannual predictability, define the physical template that has shaped organismal adaptations and ecosystem processes over evolutionary timescales (Jardine et al., 2015; Lytle & Poff, 2004; Ruhi et al., 2018). Large reservoirs can dampen seasonality by reducing both intra-annual (seasonal) and inter-annual variability, in order to satisfy demands associated with a particular unnatural timing (e.g., releases for irrigated agriculture during the growing season). In turn, small reservoirs may individually contribute little to alteration of flow seasonality; however, their cumulative effect could be large—each potentially shifting further the regulated hydrograph relative to the reference one. Characterizing how altered seasonality accumulates over space is thus consequential, and requires examining whole river networks rather than following the more traditional approach of focusing on pairs of gages upstream-downstream of reservoirs.

Here we sought to understand spatial patterns in flow regime alteration across a highly regulated river network. We asked three questions: (a) How does flow-regime alteration propagate across the river network due to flow regulation by dams of varying sizes and purposes, and the incorporation of free-flowing or less-regulated tributaries?; (b) Which dam characteristics (e.g., purpose, size) versus network-level context (e.g., location in the network, "inherited" upstream impacts) are associated with individual contributions to flow-regime alteration?; and (c) Can we combine data on dam contributions to flow-regime alteration and ecological context (flow-dependent biodiversity patterns) to evaluate potential for flow-regime restoration?

While this is not the first attempt to quantify cumulative effects of dams over space (Grill et al., 2015; Richter et al., 1998; Singer, 2007; Wu et al., 2018; Yang et al., 2008), we build on existing work in three different ways. First, we focus on a large river network spanning eight Strahler river orders and a complex array of dams and tributaries with significant demand for multiple purposes, as opposed to a single main stem with a cascade of dams. Second, we use observed, high-quality discharge time series (2003–2017) to quantify hydrologic alteration, instead of using proxies. Third, we jointly explore spatial variation in flow-regime alteration and several complementary dimensions of fish biodiversity, to assess value and risk faced by the fish communities that are sustained by regulated flow regimes. Science-informed strategies to decide where to implement environmental flows via dam releases (i.e., dam reoperation, Konrad et al., 2012; Watts et al., 2011) are critically needed given widespread river degradation and increasing trends in dam building in some of the world's biodiversity hotspots

(Winemiller et al., 2016; Zarfl et al., 2015). We show that dam reoperation could be prioritized by understanding spatial variation in flow alteration, contributions of individual dams and network structure to such alteration, and overlap between contributions to alteration and riverine biodiversity at risk.

2. Methods

We first created a spatial stream network combining flowlines and dams for the entire Colorado River Basin (CRB). For a set of 24 sites with available reference ("naturalized-flow") data, we compared observed (historical) streamflow time series to reference values. We subsequently expanded our analysis to include all possible dams or groups of dams with gages nearby (upstream-downstream), we assessed contributions to flow-regime alteration, and explained variation in contributions to alteration as a function of local dam attributes and network level descriptors. Finally, we combined these data with spatial patterns of fish biodiversity, and identified dams that could exhibit high scope for reoperation. Below we describe the details for each of these steps.

2.1. Context

The Colorado River flows for about 2,300 km, starting in the central Rocky Mountains and extending over the U.S. states of Wyoming, Colorado, Utah, New Mexico, Nevada, Arizona, and California, to finally flow into the Gulf of California in northwest Mexico (Figure S1 in Supporting Information S1). At its mouth in the Colorado River Delta, the river has a total drainage of 640,000 km^2, an area mostly covered by subarid and arid deserts (Sonoran and Mojave) and the Colorado Plateau (Figure S1 in Supporting Information S1). Native Americans have inhabited the CRB for at least 8,000 years, and today 29 federally recognized tribes depend on the river. Over 40 million people, both within and outside the basin, benefit from its water for municipal use and irrigation. For management purposes, the CRB is divided into two sections: the Upper CRB, upstream of Lees Ferry (near Glen Canyon Dam), and the Lower CRB, integrating watersheds downstream of Glen Canyon Dam. The Upper and Lower CRB have distinct hydroclimates. The Upper CRB receives a relatively even distribution of precipitation year-round, and flow is controlled by snowmelt runoff, which is in turn determined by snowpack over the antecedent cold season (Christensen et al., 2004). In contrast, the Lower CRB (except for the main stem) exhibits a sharp peak over the summer monsoons and a secondary peak created by frontal storms in the winter (Sheppard et al., 2002). Glen Canyon dam, in operation since 1963, and Hoover Dam, in operation since 1936, are two of the largest reservoirs by volume in the U.S. and provide most of the river's hydropower production. The Colorado River system is operated under the "Law of the River," a complex set of legal documents (e.g., treaties, compacts, statutes, regulations, and contracts) that are relevant to the allocation and management of waters in the CRB. A decline in river flows by nearly 20% (on average) relative to pre-dammed conditions, and ongoing climate-driven supraseasonal droughts, have led to overallocation of resources and significant management challenges (Butler et al., 2021). From an ecological standpoint, the CRB has some of the most unique and endangered fish communities in North America, resulting from long isolation and strong environmental gradients (Minckley & Deacon, 1968). At the same time, over the past 150 years the basin has become highly invaded, partly due to "niche opportunities" provided by reservoirs and associated alterations of flow and thermal regimes (Olden et al., 2006; Ruhí et al., 2016).

2.2. Selecting Dams and Gages

We started with a selection of 1,445 dams from the U.S. Army Corps of Engineers *National Inventory of Dams* database (Goteti & Stachelek, 2016), spanning both the Upper and Lower CRB. We focused on intermediate to large dams, with height >12.2 m (40 feet) or storage capacity >1.23 million m^3 (1,000 acre-feet), per the American Society of Civil Engineers definition. Next, we identified a total of 1,749 streamflow gaging sites in the basin from the U.S. Geological Survey's National Water Information System. Discharge series were obtained using the *dataRetrieval* R package (Hirsch & De Cicco, 2015). In order to be included in the analysis, gaging stations had to be located in streams (e.g., excluding those in springs or wells), and had to report mean daily discharge records for at least 15 years continuously (2003–2017). Using these conditions, we identified a total of 239 stations. We then used the NHD*Plus*v2 data set (McKay et al., 2012) to characterize the CRB stream network. In particular, we used the River and Infrastructure Connectivity Network data set (Mukhopadhyay et al., 2020) that merged three data sets (on streamgaging sites, dams, and river flow lines), to create a data tree in which each node represents individual reservoirs and connecting stems represent river reaches in-between those reservoirs. In this merged network, point information is stored as attributes of either nodes (reservoirs) or stems (streamgages). This method relies on the "Value Added Attributes" of the vector processing units in the NHD*Plus*V2 data set (McKay et al., 2012), which are useful for upstream to downstream navigation and analysis. The algorithm first identified the nearest river reach of each point feature (dam or a gage), and then linked points based on attributes of the nearest flowline. The developed final network for the CRB was verified with previous publications (Christensen et al., 2004; Richter et al., 1998; Woodhouse et al., 2006) and the United States Bureau of Reclamation (USBR) reports. The final network had, for each reservoir, information on (a) dams immediately upstream, (b) dams immediately downstream, (c) gages between the focal dam and upstream dams, (d) gages between the focal dam and downstream dams, and (e) distance (in kilometers) between each pair of nodes (reservoirs, gages, or a combination of the two). Collectively, this procedure allowed analyzing the effects of 42 "clusters" of dams (i.e., individual dams or small groups of dams that did not have a gage in between), encompassing 84 intermediate-to-large structures (Table S1 in Supporting Information S1). These 84 dams (out of the 1,445 in the basin) account for the vast majority (83.3%) of storage in the basin, according to the total reservoir storage across the CRB calculated from the USACE National Inventory of Dams (Goteti & Stachelek, 2016). These selected dams had a median height of 30 m and median storage capacity of 27.5 Mm^3.

2.3. Comparing Naturalized to Observed Flows

As a first step toward understanding how flow regime alteration propagates across the river network, we aimed to compare time series of observed flows to reference ("naturalized") flows for a subset of 24 sites for which natural flow reconstructions were available. We used the USBR Colorado River Basin Natural Flow and Salt Data (www.usbr.gov/lc/region/g4000/NaturalFlow/current.html), which uses time series of human consumptive water use and water loss to compute natural flow at a monthly scale. In particular, USBR uses 9 categories of reported consumptive use (e.g., irrigated agriculture, municipal and industrial, thermal power) in the Upper basin, along with available source data; a similar process is followed for the Lower basin using decree accounting. Time series of consumptive uses and losses along with reservoir regulation policy and observed flows were then inputs to the RiverWare software, a simulation/optimization tool that generates naturalized flows. The naturalized flows inform long-term (decadal) planning in the USBR Colorado River Simulation System, and have been used in research on the effects of hydroclimatic variability on flow regimes.

Comparing the observed and reference flow series, we then quantified flow alteration based on four different dimensions: (a) mean annual streamflow; (b) seasonality; and wavelet coherence at the (c) seasonal scale and (d) annual scale. We quantified flow seasonality using the Seasonality Index, *SI* (Markham, 1970). This index translates mean monthly hydrological data (streamflow in this case) into vector quantities—magnitude being the monthly measurand, and direction being the month of the year expressed in arc-units. The magnitude of the resultant vector (after summing the 12 monthly vectors) is a measure of seasonality, and its direction captures peak timing. The ratio of the resultant vector magnitude to the total mean annual quantity is the *SI*, and values range between 0 and 1. *SI* values close to 1 reflect situations where most flow is concentrated in a single month, whereas values close to 0 indicate an even distribution throughout the year (see Petersen et al., 2012 for an application on streamflow). To assess whether reference and observed streamflows at a given station differed in seasonality, we compared their values ($SI_{reference}$ - $SI_{regulated}$), creating a variable we named *SI loss*. We then mapped and assessed spatial variation in *SI loss,* to assess whether some dams had been dampening flow seasonality (relative to reference, free-flowing conditions) more than others, and whether *SI loss* was "inherited" downstream.

In addition to *SI*, we used Wavelet Coherence (*WC*) to assess the association between reference and observed time series in both the time and frequency domains (Grinsted et al., 2004; Torrence & Webster, 1999). Given two time series *X* and *Y*, their *WC* can be described as:

$$WC = \frac{|\left\langle a^{-1} W_b^{XY}(a) \right\rangle|^2}{\left\langle a^{-1} |W_b^X(a)|^2 \right\rangle \cdot \left\langle a^{-1} |W_b^Y(a)|^2 \right\rangle} \quad (1)$$

where $W_b^{XY}(a)$ is the cross-wavelet spectrum of two time series, a is the scale parameter, b is the localized time index, $W_b^X(a)$ and $W_b^Y(a)$ are the wavelet spectra of X and Y, respectively. The notation $\langle \cdot \rangle$ indicates smoothing in both time and scale. *WC* values range from 0 to 1; the more coherent two time series are in terms of frequency and timing, the closer *WC* is to 1 (Torrence & Webster, 1999). To assess the association between reference and observed streamflows in terms of their periodicity over the study window (2003–2017), we computed the mean WC between observed and reference flows by averaging their WC spectrum over the corresponding 15-year window. We allowed for some uncertainty around each target periodicity. In this vein, for WC at the seasonal scale the band was centered around 6 months (±2 months, thus spanning 4–8 months); for WC at the annual scale, the band was centered around 12 months (±2 months, thus spanning 10–14 months) (for more details, see Hwang et al., 2021).

2.4. Modeling the Spatial Network of Dams and Observed (Historical) River Flows

Our main goal was to explain how flow alteration propagates across the river network, and to understand how dam attributes (e.g., size of the reservoir, purpose of the dam; see Table S2 in Supporting Information S1) contribute to such patterns. Consequently, we explored a multilevel modeling framework that allows for the structuring of observed (historical) streamflow information sequentially in the entire basin. Since streamflow on a convergent dendritic river network can be described by a spatial Markov process, we modeled the whole river basin as a spatial network with flow at a downstream gage being informed by flow at the gage immediately upstream; and reservoirs potentially reducing flow variability at various time scales depending on degree of regulation, purpose, and operational constraints. We started from the terminal (i.e., most downstream) gage on the Colorado River main stem, the Colorado River at the North International Border Above Morelos Dam, AZ (USGS #09522000), and moved upstream. Expected monthly flows at the terminal gage were then modeled using monthly flows of its immediate upstream gages, in a generalized linear modeling framework. We repeated this process for each gage, sequentially along the basin, moving from terminal to headwater positions in the river network. This sequential identification of downstream (response) and immediately upstream gages (predictors) resulted in 117 response-predictor(s) sets (i.e., pairs of stations that are immediately upstream or downstream of each other). Log-transformed monthly streamflows were normally distributed, and log-linear models sufficed for describing the conditional relations of downstream versus upstream flows. The mathematical representation of the spatial network models is:

$$\ln\left(y_t{}^{(i)}\right) = \alpha_i + \sum_{j=1}^{m} \beta_i^{(i_j)} \ln\left(y_t^{(i_j)}\right) + \epsilon_t^{(i)} \ldots, \quad (2)$$

where subscript t is a time-varying index representing monthly time steps, superscript (i) represents the station being modeled, and i_j indexes the subset of gages that are identified to be immediately upstream of gage i. j runs from 1, ..., m if i is informed by m number of gages upstream. The monthly streamflow data $y_t^{(i_j)}$ that act as upstream "feeder" for a downstream gage i are weighted by regression coefficients $\beta_i^{(i_j)}$. The subscript on the regression coefficients represents the downstream gage being modeled, and the superscript represents the specific upstream feeder gage. The intercept term is α_i, and $\epsilon_t^{(i)}$ is the model error term. The intercepts and regression coefficients were estimated via maximum likelihood with the observed flow data. Then, R^2 were computed for each model to obtain an estimate of the amount of variance in the downstream gage $y_t{}^{(i)}$ that could be explained using the gages immediately upstream $y_t^{(i_j)}$. High R^2 values indicate flows between upstream and downstream portions of the basin varying synchronously—thus, a low degree of alteration. In contrast, low R^2 values indicate that dams dampen or shift seasonality. We illustrate our approach conceptually and statistically (using a directed graph) in Figures 1a and 1b.

We hypothesized that spatial variation in R^2 (i.e., variation in contributed alteration) should be explained by a combination of local and contextual attributes. Local variables considered include the number of dams of different types in the reach, their cumulative storage, their primary and secondary purpose, their degree of regulation, their number of upstream feeder gages, and the average distance between the upstream and downstream portions of the basin being analyzed (see complete list in Table S2 in Supporting Information S1). In turn, contextual variables integrate the upstream network—from the gage of interest to the headwaters. These context-level variables included the upstream number of dams of various types, their total storage, stream order, and the proportion of flow at the downstream gage that was controlled by dams (see complete list in Table S2 of Supporting Information S1). We used the regression-based technique known as Least Absolute Shrinkage and Selection Operator

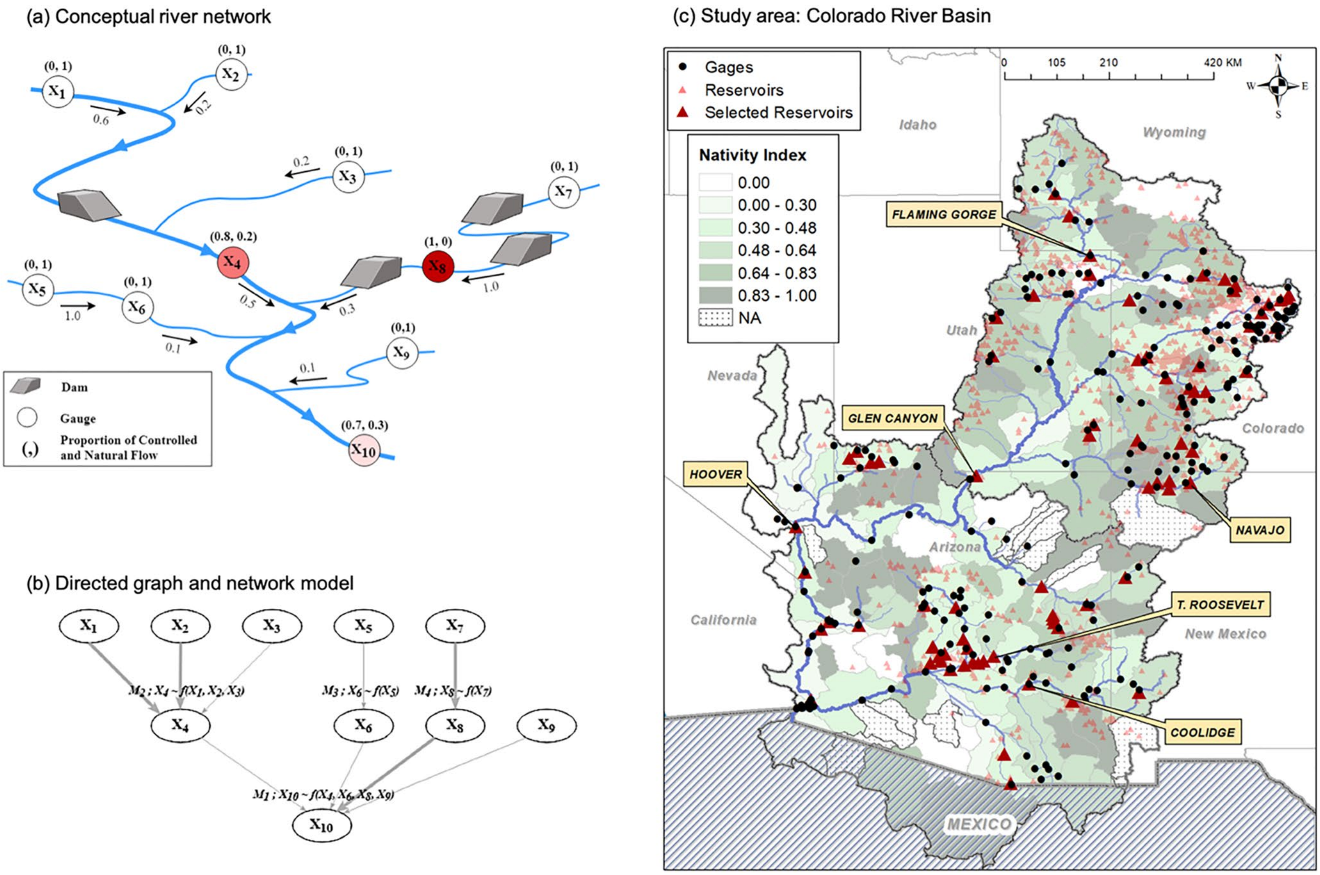

Figure 1. (a) Conceptual diagram illustrating the cumulative effects of dams on river flow regimes, as water flows downstream the riverine network. The proportion of controlled and natural flows changes progressively as dams accumulate, and as free-flowing tributaries join the highly-regulated main stem. (b) Associated directed graph operationalizing the conceptual diagram (a) into a statistical model. Nodes (gages) are connected via links. Link strength is a measure of dam contributions to flow alteration—if a dam fundamentally disrupts the flow regime, our ability to predict downstream flows from flows immediately upstream decreases. (c) Spatial distribution of gages and reservoirs across the Colorado River Bain (CRB). A total of 84 large reservoirs were considered in this study (red triangles), representing >83% of the total storage in the CRB. Watershed (HUC8-level) shading represents the proportion of the fish community represented by native species, as a proxy for ecological integrity.

(LASSO) to identify the best set of local and contextual variables that explained spatial variation in R^2. LASSO assumes a Gaussian linear relationship between responses and predictors, but adds a constraint to the regression coefficients in least-squares optimization that conveniently leads to dropping unnecessary variables. Including this constraint results in the shrinkage of certain coefficients to zero, providing a way to identify the best predictor subset. Variables associated with coefficients that were shrunk to zero were dropped. The remaining variables were classified in local versus contextual, and ranked based on their relative importance (Grömping, 2006).

2.5. Mapping Fish Biodiversity and Dams With High Scope for Reoperation

We mapped fish biodiversity at the watershed level (i.e., Hydrologic Unit Code 8, or *HUC8*) across the CRB. We focused on three metrics: (a) the proportion of native species within each HUC8 (i.e., *fish nativity*); (b) the *fish conservation value*, calculated as the number of species of conservation concern present in that HUC8 (i.e., total number of Critically Endangered, Endangered, Vulnerable, and Near Threatened species); and (c) the *seasonal dependency* of each fish assemblage, calculated as the proportion of species adapted to seasonal flow regimes (Mims & Olden, 2012), that is, the aggregated share of *opportunistic* and *periodic* strategists. The list of species and origin (native vs. non-native) per HUC8 was obtained through NatureServe (Natureserve, 2018) and the U.S. Geological Survey's Non-indigenous Aquatic Species database (USGS, 2018), after excluding records from lentic systems and from non-self-established populations (e.g., eradicated or stocked populations, populations with failed establishment, vagrant species). Species names were harmonized to the species level, according to the

Catalog of Fishes (Eschmeyer et al., 2017), and their global conservation status was retrieved from the IUCN Red List (IUCN, 2019). We classified species according to the life-history triangle of Winemiller and Rose (1992), which uses the endpoints of the three-dimensional space defined by age at maturity, fecundity, and parental care (Olden et al., 2006). We defined as *periodic* strategists those fish species with late maturation, high fecundity, and low juvenile survivorship—traits that are beneficial in seasonal environments. We classified as *opportunistic* fish species those with early maturation, low fecundity, and low juvenile survivorship—advantageous traits in frequently-disturbed ecosystems. *Equilibrium* strategists were fishes with intermediate maturation age, low fecundity, and high juvenile survivorship—traits that are favored under environmental stability (Olden et al., 2006; Winemiller & Rose, 1992). Instead of assigning fish species to a single category, we used a soft classification system based on affinities, using the inverse of the Euclidean distance between each species position and the strategy endpoints (standardized between 0 and (a). This approach accommodates species that fall between categories by assigning species with affinities between 0 and 1 for each category. The seasonal dependency of the fish assemblage in a given watershed was then obtained using the proportional species richness of flow-dependent strategies, using the ratio of the summed affinities for the opportunistic and periodic strategies across all species in that HUC8 by the total sum of affinities.

Finally, we ranked individual dams (i.e., from first to last) in different dimensions: their contributed flow-regime alteration (i.e., low to high R^2), the amount of downstream dam-free habitat, and each of the three facets of fish biodiversity described in the previous section. By identifying dams that ranked high in different dimensions we showed that some dams deserve further examination to be reoperated, as restoring flow regimes via seasonal releases from reservoirs could potentially deliver higher hydro-ecological benefits.

3. Results

3.1. Comparing Natural to Regulated Flows Across the River Network

We applied the network model to the whole Colorado River Basin (CRB), which allowed for quantifying propagation of flow alteration (Figures 1a and 1b) from the headwaters to the strongly regulated, non-native-fish-dominated main stem (Figure 1c). Our selection of intermediate to large dams captured regulation in major tributaries such as the Green River (Flaming Gorge Dam), San Juan River (Navajo Dam), Salt River (Theodore Roosevelt Dam), and Gila River (Coolidge Dam); as well as in the Colorado main stem (e.g., Glen Canyon and Hoover Dams, Figure 1c).

Comparing reference to observed flow characteristics using a subset of sites with naturalized flow series (i.e., the 24 sites with flow estimates from the U.S. Bureau of Reclamation representing free-flowing conditions), we found that most dams fell relatively close to the 1:1 line when considering mean annual flows (Figure 2b). In contrast, flow seasonality was strongly altered by the presence of dams across the basin (Figure 2c). Deviations from expected seasonality were stronger in higher river orders, suggesting that flow alteration tended to accumulate along the river network (Figure 2c). Hydropower and flood control dams showed the strongest deviations.

A more detailed examination of observed versus naturalized hydrographs across the network confirmed that sites in the lower main stem of the Colorado River were less seasonal because they had their seasonality dampened by regulation (i.e., high values for *SI Loss*; Figure 3). In turn, sites with low levels of *SI loss* generally had no or low levels of regulation (e.g., *n9*, Yampa River near Maybell, Colorado; *n17*, Paria River at Lees Ferry, Arizona; *n18*, Little Colorado River near Cameron, Arizona; *n19,* Virgin River at Littlefield, Arizona). Sites in the lower Colorado mainstem had virtually flat hydrographs instead of the peaks in late spring and early summer that characterize natural flow regimes in that part of the network (Figure S2 in Supporting Information S1). Glen Canyon dam strongly dampened flow seasonality (Figure 3, station *n16*), and main-stem flow regimes recovered minimally for the whole lower stretch of the Colorado River (Figure 3; Hoover, Davis, Parker, and Imperial Dams, stations *n20, n21, n23*, and *n24*).

We then assessed wavelet coherence between natural and observed flows (*WC*), describing association between the two in the time-frequency domain at the local level, and we compared it to R^2, a measure of flow alteration based on the spatial network model. These analyses allow for understanding the different signatures of flow alteration by dams, which may include a combination of altered flow magnitude, flow variability, and timing of high and low flows (Figure 2a). We found that R^2 did not closely track coherence between observed and expected flow regimes at seasonal or annual scales (Figures 2d and 2e): many dams (particularly those operated

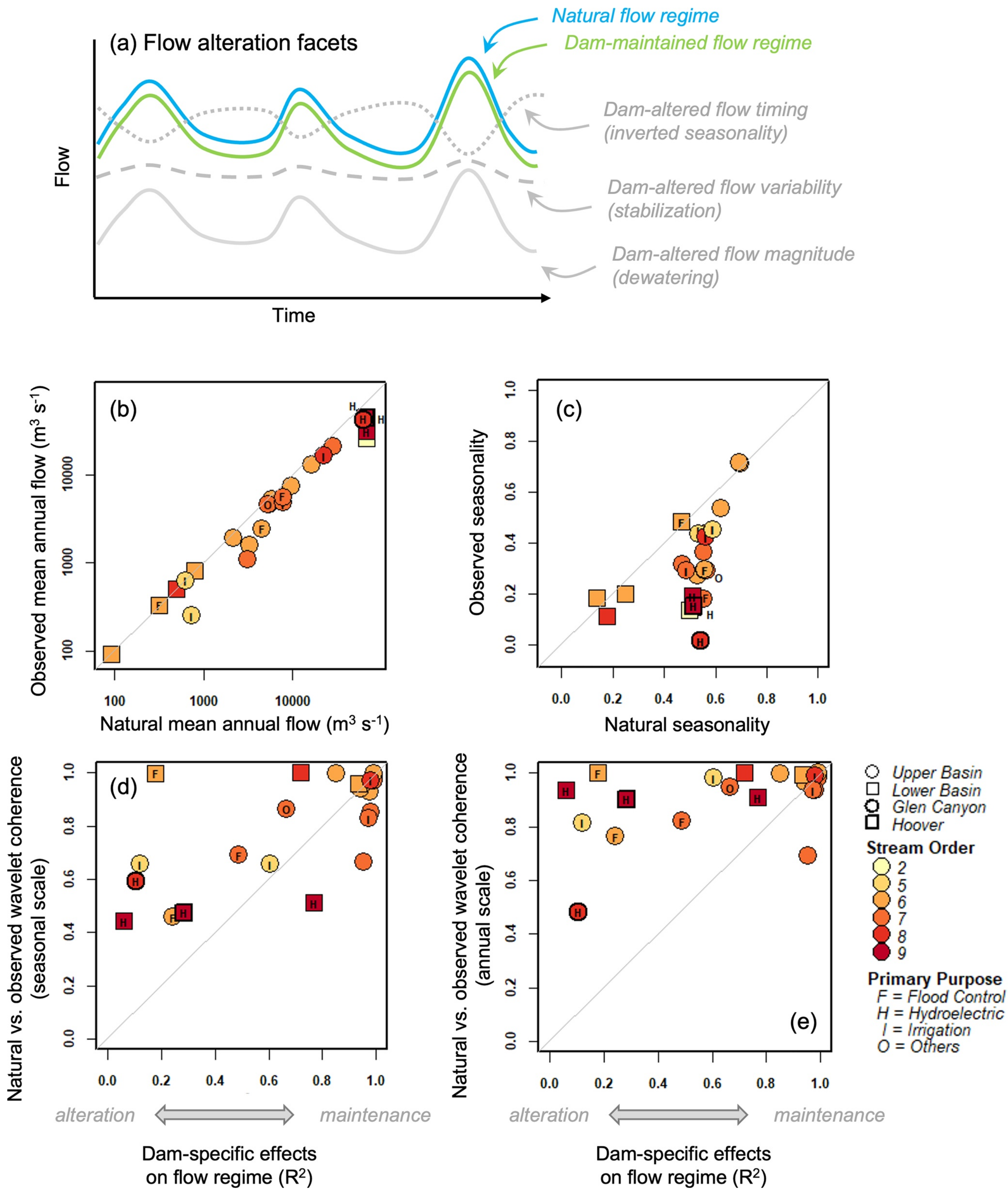

Figure 2. (a) Potential facets of flow regime alteration: dams may mimic the natural flow regime (green line), or may contribute flow alteration by changing the magnitude, variability (frequency and/or amplitude), and timing of high and low flows—as shown with gray lines. (b and c) Comparison of natural (reference flow series) and observed flows at 24 sites across the Colorado River Bain, with regards to (b) mean annual flows, and (c) seasonality index (see Methods for details). (d and e) Relationship between dam effects of dams (as measured by R^2; the lower, the more impactful the dam), and wavelet coherence metrics at the seasonal and annual scale. Shapes indicate the location of gaging stations in the basin, and gages located downstream of the two largest dams in the system (Glen Canyon and Hoover dams) are bolded. Primary purpose is also indicated, when gages were immediately downstream of a dam or cluster of dams.

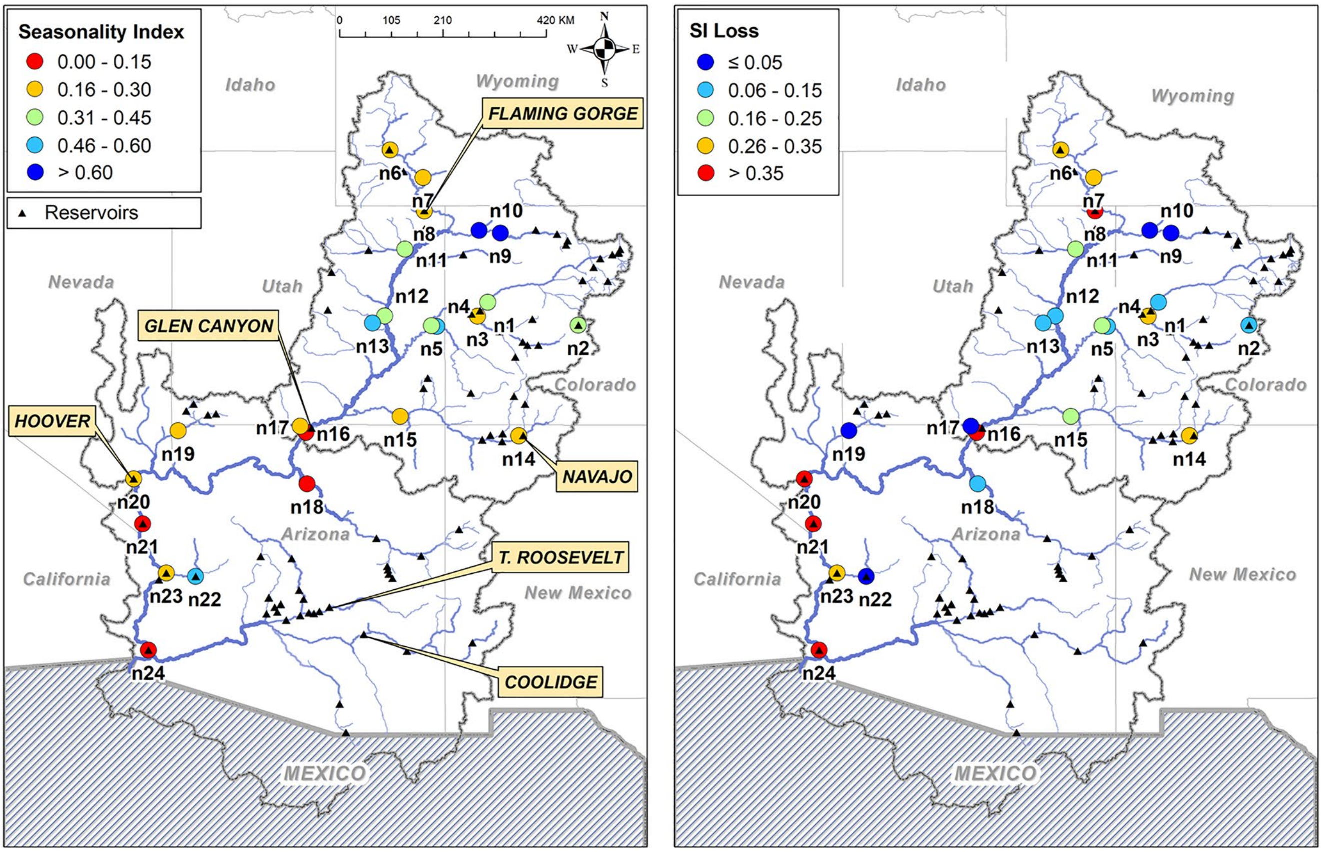

Figure 3. Spatial patterns in observed flow seasonality (Seasonality Index, *SI*) and in changes in flow seasonality (*SI loss*), across the Colorado River Basin. *SI loss* values result from comparing SI on observed relative to naturalized flows—the higher the *SI loss* values, the stronger dams and/or human activities have been dampening flow seasonality relative to reference, free-flowing conditions. The observed and naturalized-flow hydrographs for each station, and the corresponding USGS gaging station codes, are shown in Figure S2 of Supporting Information S1.

for hydropower production) had lower-than-expected R^2 values if they received flow regimes that were already dampened (Figures 2d, 2e and 3). Again, hydropower and flood control dams presented the highest rates of *WC* loss and R^2 alteration derived from the spatial network model (Figures 2d and 2e). These results suggest that even if mean annual flows were preserved across the system, losses in flow seasonality and variability accumulated, as expected in a system regulated by multi-year reservoirs.

3.2. Spatial Variation in Flow Alteration: Local Versus Network-Level Controls

Expanding our analyses to the full set of stream gages available across the CRB, the spatial network model results showed a wide range of dam effects on flow alteration, measured here as R^2 (Figure 4a). Flow alteration values ranged between 0.03 and 0.99 (mean ± SD: 0.54 ± 0.33), and spatial variation in these values was consistent with the previous observation that alteration tended to increase downstream. Most headwaters started with no or low levels of flow alteration, and R^2 dropped with sequential addition of dams in the network. However, some exceptions to this pattern existed. In some headwaters, dams showed higher R^2 than upstream counterparts, indicating little cumulative effects. In other cases, low R^2 were not associated with flow regulation (e.g., in the free-flowing San Pedro River), likely indicating other sources of flow regime alteration (e.g., groundwater abstraction).

When assessing the role of local versus contextual (i.e., network-level) variables via LASSO regression, we found that spatial context was almost twice as important as local attributes in explaining variation in dam contributions to flow alteration (63% vs. 37% of explained variance) (Figure 4b). Among the contextual (i.e., network-level) variables, dam location and the number of upstream flood control dams were the most important ones in explain-

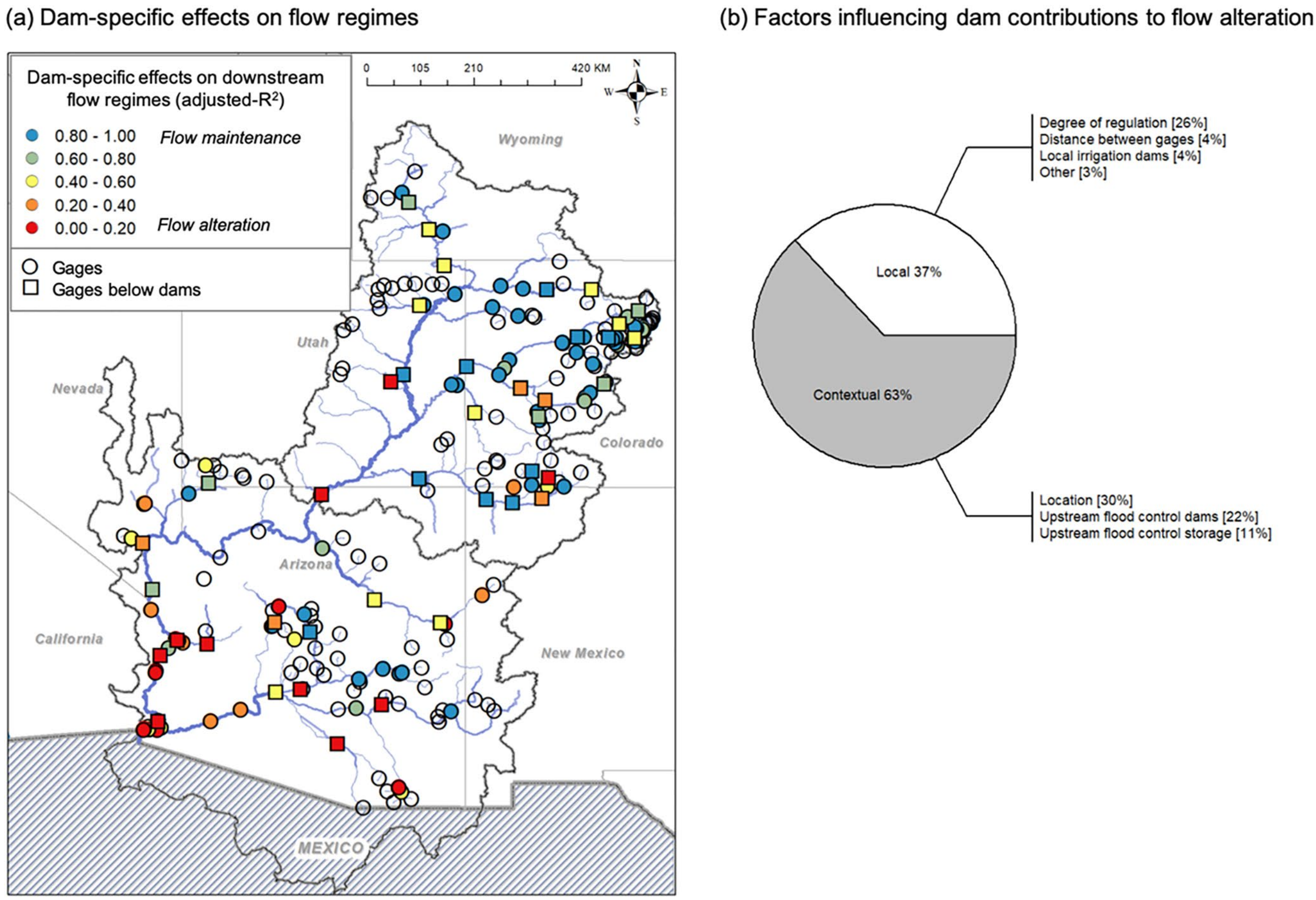

Figure 4. (a) Results of the network model quantifying effects of dams on the flow regime across the Colorado River Bain (Figure 1). High R^2 values represent flow maintenance, or a dam not altering substantially a flow regime. Low R^2 values capture flow alteration, or a dam shifting the magnitude, variability, and/or timing of flows (Figure 2). Terminal gages (i.e., those most upstream in a branch, thus without an upstream pair to be compared to) are represented as transparent circles. (b) Results of the Least Absolute Shrinkage and Selection Operator regression model identifying local and contextual variables that explain variation in R^2 values. See Methods for more details, and Table S2 in Supporting Information S1 for a complete list and description of the local and contextual variables considered in the study.

ing spatial variation in dam-contributed flow alteration (Figure 4b). Detailed analysis of the contextual and local variables showed the direction and statistical significance of their effects (Figures 5a and 5b, Table S3 in Supporting Information S1). Specifically, dams with higher contributions to alteration were significantly associated with a higher total volume relative to mean annual streamflow (degree of regulation; Figure 5a, Table S3 in Supporting Information S1), and were located in the Lower Colorado main-stem or in areas in the Lower CRB with high cumulative numbers of flood control dams (Figure 5b).

3.3. Fish Biodiversity Patterns and Spatial Prioritization

Finally, the spatial prioritization exercise revealed that 19 out of the 42 dam clusters ranked highly in contributions to flow alteration while being located in watersheds with high biodiversity values—either in terms of native fish representation (*nativity status*), presence of endangered species (*conservation value*), or proportion of the fish community that depends on seasonal flow regimes (*seasonal dependency*) (Figure 6). We note that these three dimensions of biodiversity were largely complementary over space (mean Pearson's $r = 0.18$), making their simultaneous maximization challenging. While fish communities were mostly represented by species that benefit from variable and/or seasonal flow regimes (mean: 71%, range: 58%–78%), we observed wide variation in native representation (mean: 45%, range: 13%–89%) and in the absolute numbers of endangered and threatened species per watershed (mean: 3.4, range: 0–9).

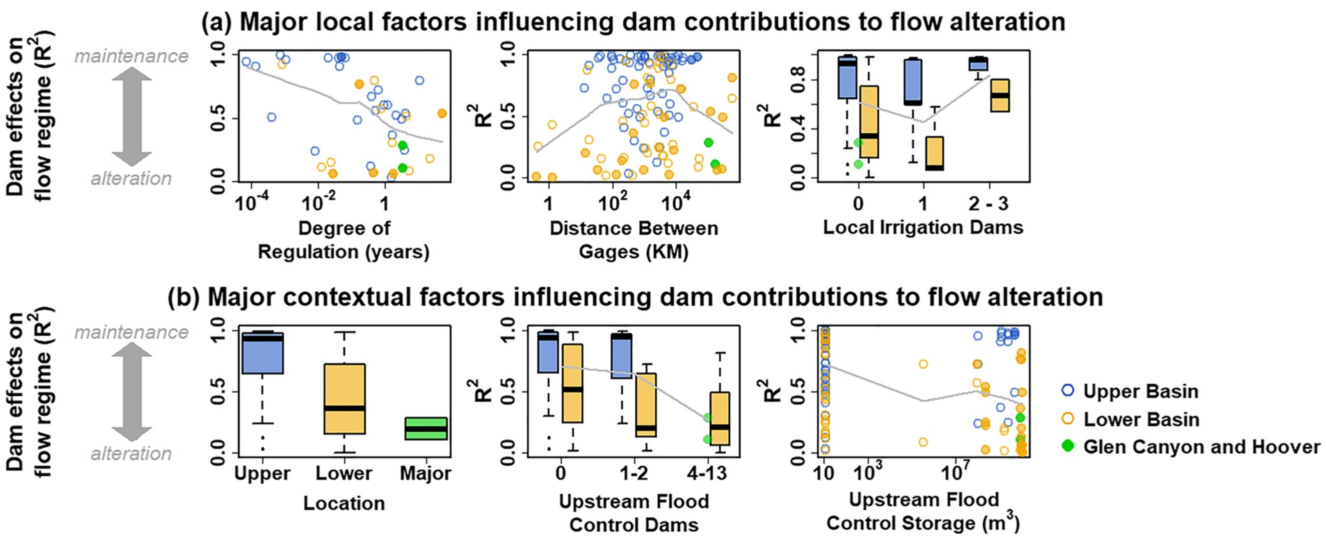

Figure 5. Association between R^2 values, representing dam effects on flow regimes, and major local (a) and contextual variables (b), as identified by the Least Absolute Shrinkage and Selection Operator (LASSO) regression model. Colors indicate whether gaging stations are located in the Upper Colorado River Bain (CRB), Lower CRB, or immediately downstream of the two largest dams (Glen Canyon and Hoover dams).

Importantly, dams differed widely in distance to the closest downstream dam or cluster of dams, with values ranging between 2 and 1,111 km (mean ± SD: 285 ± 295 km; see variation in bubble size in Figure 6). This result suggests that flow restoration via dam reoperation could have widely ranging benefits across dams, as eventual flow releases by single dams would often, but not always, be constrained by dams downstream. Among the subset of highly impactful dams, Flaming Gorge Dam (Green River) and Glen Canyon Dam (Colorado River main stem) were the two dams with the longest stretches of downstream dam-free habitat, and were also located in watersheds with above-median conservation value and risk—the latter defined by fish communities dependent on seasonal flow regimes that are no longer present.

4. Discussion

Dams, together with other major drivers of flow regime alteration such as urbanization and climate change, have deep impacts on riverine biodiversity, mainly by dampening and homogenizing flow variability, by fragmenting the riverine and riparian habitat, and by facilitating biological invasions (Bunn & Arthington, 2002; Johnson et al., 2008; Palmer & Ruhi, 2019). Despite a long history of research on dam-induced hydrologic alteration and its ecological impacts (Poff, 2018; Poff et al., 2010), most work has been developed at small spatial scales and has focused on operation of single dams—or at larger spatial scales, but considering individual dams as "replicates". Modeling spatial dependencies among dams is necessary to assess cumulative dam impacts across a stream network, variation in how individual dams may contribute to downstream alteration, and potential recovery of flow variability by the incorporation of unregulated tributaries. Here we examined the propagation of dam-induced flow alteration in the highly regulated Colorado River Basin, and identified local and network-level controls of alteration. We found that flow alteration tended to accumulate along the network, and seasonality did not recover despite the incorporation of less-regulated or free-flowing tributaries. Additionally, contextual (network-level) factors explained almost twice as much variation in contributions to alteration (63%) than variables associated with the particular dam being analyzed, or with the local river reach (37%). Our results build on previous research showing the important cumulative effects that dams have over space (Grill et al., 2015; Poff et al., 2007; Richter et al., 1998; Singer, 2007; Wu et al., 2018; Yang et al., 2008), and advance the notion that mitigating flow alteration—and its ecological impacts—requires considering river network context-dependencies. We further show that this better understanding of river network context could help advance environmental flow planning by identifying infrastructure with high scope for reoperation (sensu Grantham et al., 2014).

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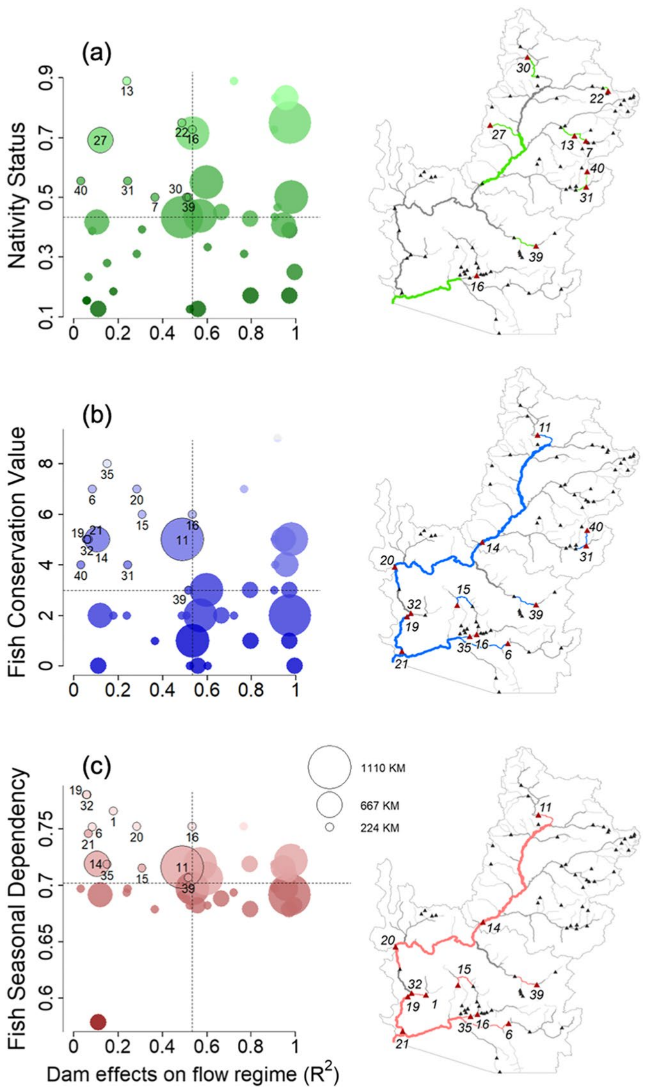

Figure 6. Spatial prioritization exercise identifying dams with high reoperation scope at the river network scale. We combine three dimensions: the effects of dams on flow regimes (x-axes; the lower, the more disruptive is the dam), the distance to the nearest downstream dam (bubble size; the bigger, the longer is the river segment that would benefit from flow regime restoration), and fish biodiversity as a proxy for ecological value (y-axes). Fish biodiversity was examined using three complementary facets: (a) proportion of native fish species found in the watershed (the higher, the better preserved the community); (b) fish conservation value, measured as the number of species of conservation interest (including Critically Endangered, Endangered, Vulnerable, and Near Threatened; the higher, the greater are the potential ecological benefits of flow regime restoration); and (c) fish dependency on seasonal flows, measured as the proportion of species adapted to variable flow regimes (opportunistic + periodic life-history strategists; the higher, the more vulnerable is the fish community to flow stabilization by dams). Code labels identify dams or dam clusters that are both hydrologically impactful and have high ecological value (relative to the respective median as illustrated by the dotted lines). See Methods for details, and Table S1 in Supporting Information S1 for dam cluster codes.

4.1. Flow Alteration Is Context-Dependent and Propagates Downstream

Flow variability was more sensitive than flow magnitude to the cumulative effects of upstream dams, a pattern explained by downstream sections receiving alteration from multiple upstream dams and "inheriting" a diversity of flow alteration signatures. Flow seasonality was particularly low in main-stem sites downstream of Glen Canyon Dam (Figure 3), and the difference between flow seasonality under expected (i.e., naturalized) versus observed flows remained high across the whole downstream section—indicating that the amplitude of fluctuations in monthly flows between low-flow and high-flow seasons would be consistently higher under free-flowing conditions. It is important to note that this "inherited" alteration persisted despite the incorporation of highly-seasonal tributaries such as the Paria, Little Colorado, Virgin, and Bill Williams Rivers (Figure 3 and S2 in Supporting Information S1; stations *n17-19* and *n22*). This observation suggests that seasonal flow pulses from the tributaries were unable to make significant contributions to restoring natural flow variation in the main stem, as these tributaries contribute a small fraction of the mainstem monthly streamflow. Another ecologically-meaningful facet of flow alteration was the *timing* of low and high flows. In this case, we observed substantial advances in peak flow timing along the section that underwent the strongest flow stabilization (i.e., stations *n20*, *n21*, *n23*, and *n24*; Figure 3). That river section exhibited small, smooth peaks in flow in March-April instead of the large peaks in May-June that would result from snowmelt under free-flowing conditions (Figure S2 in Supporting Information S1). The alteration in peak flow timing likely relates to the timing of downstream water needs, particularly for irrigated agriculture, which continues to be the largest use in the CRB with more than half of the total consumptive use basin-wide (Butler et al., 2021).

We also examined dam contributions to flow-regime alteration, and identified drivers that explained variation in these contributions (local vs. contextual or "landscape" level, Poff & Hart, 2002). The finding that local conditions and dam properties were important supports abundant research showing that large dams, particularly hydroelectric ones, are very impactful to flow regimes and riverine biodiversity (Barbarossa et al., 2020; Chalise et al., 2021). We note here that at shorter timescales (e.g., daily and subdaily scales), these patterns would have likely become even more apparent, given we did not consider alteration that may take place at finer scales than monthly (e.g., hydropeaking, Kennedy et al., 2016). However, we also found that context was almost twice as important as local dam characteristics (63% of the explained variance in the LASSO regression). We suggest two factors may explain this pattern. First, important management differences exist in the Upper versus Lower Colorado River Basins, and in the amount of water that is actively allocated (and thus "moved" from wet seasons to dry seasons) in each of the two management units. While the Upper Basin uses about half of its 7.5-million-acre fit allocation, demand in the Lower Basin grew hit its full apportionment by the late 1990s (Butler et al., 2021). The fact that most flow is accounted for, and the high degree of regulation and water residence time of the large dams in the lower Colorado main-stem (Kumar et al., 2022), likely decreases R^2 values by temporally decoupling inputs and outputs at each reservoir. This may take place if water is released to fulfill downstream needs when inputs during that particular month do not increase; or if inputs at the reservoir level are diverted or used, and are thus not reflected as outputs (leading to a temporal decoupling or asynchrony, and hence a low

R^2). Accordingly, the location of the reservoir being examined (Upper vs. Lower basin, or immediately downstream of the two largest dams, Glen Canyon and Hoover) had a strong influence on the contributed flow regime alteration. Second, because alteration propagates downstream, it is expected that the marginal impact of a dam depends on the degree of regulation of all upstream dams. This expectation is consistent with the fact that cumulative flood-control dams (upstream storage and number of dams) were selected as two of the main context-level variables (with a collective explanatory power of 33%). Flood-control storage is known to dampen flow variance (particularly pulse flood flows, FitzHugh & Vogel, 2011), but that is largely a non-consumptive use—unlike water supply and irrigation dams, which are more likely to shift timing and reduce flow magnitude via abstraction and diversions. Thus, it was expected that network-wide flood-control storage would play a critical role in flow alteration, while water supply and irrigation dams would present more localized signatures. The observation that increased storage of irrigation dams increased R^2 in a local context (indicating flow maintenance at high levels of storage by irrigation dams) suggests the existence of similar timing of releases between upstream and downstream dams—likely to fulfill irrigation needs. In turn, this highlights the feasibility of coordinating timing of environmental flow releases across dam cascades to deliver benefits to long river sections (Ahn et al., 2018). Overall, our results underscore the significance of both local and network context for understanding flow regime alteration, and show that potential for restoring "local" flow regimes may be highly constrained by upstream impacts.

4.2. Implications for River Ecosystems

The position of a habitat in the river network is known to control biological dynamics, as downstream sites tend to accumulate aquatic organisms via downstream drift, while communities at the tips of the river network may be more controlled by environmental factors that differ across headwaters (Brown & Swan, 2010; Swan & Brown, 2017; Terui et al., 2018). Given that network position also controls flow alteration (as reported here), our results suggest that both general river network topology (e.g., branching complexity, Larsen et al., 2021) and position of the study habitat within that network should be more carefully considered when assessing flow alteration-ecology relationships. This is because not only the amount of flow alteration that a dam may contribute locally, but also its effects on biological communities, may change along the river network (in agreement with the "network position hypothesis", Brown et al., 2018; Henriques-Silva et al., 2019). While research on flow-ecology relationships has assessed transferability of such associations over space and time (Chen & Olden, 2018), the dendritic structure of river networks should be explicitly considered moving forward when examining ecological responses to flow alteration (Palmer & Ruhi, 2019; Poff, 2018; Richter et al., 1998).

Our mapping exercise (Figure 6) also showed that it may be difficult for watershed managers and conservation planners to identify dams that, if reoperated, they would optimize for multiple facets of fish biodiversity simultaneously. In our case, we found that the presence of native fish ("*nativity status*"), endangered species ("*conservation value*"), or fishes that required seasonal flow regimes ("*seasonal dependency*") did not show strong, positive correlations across sub-watersheds of the CRB. This challenges prioritization exercises that may seek to achieve these three goals simultaneously—even in the absence of considerations around dams. Efforts focusing on prioritizing watersheds for maximizing freshwater biodiversity conservation using complementarity-based algorithms have shown the challenges of optimizing for multiple groups, and the threat that flow impairment may represent to habitat in priority networks (e.g., in California, Howard et al., 2018). We note here, however, that assemblages throughout the CRB were largely represented by species that benefit from variable and/or seasonal flow regimes. Thus, it is reasonable to expect that most efforts aimed at restoring reference flow seasonality (both in magnitude and timing) may deliver net benefits, even if actual outcomes differ from watershed to watershed. Previous research has quantified how large dams dampen flow variability and effectively reduce the diversity of environments available to aquatic organisms at regional to continental scales (Comte et al., 2021; Poff et al., 2007). This flow stabilization often increases representation of non-native fishes whose "equilibrium" life histories (high parental care and aseasonal reproduction) may benefit from the absence of erratic flow variability or periodic high and low flows (Comte et al., 2021; Mims & Olden, 2013). It is thus not surprising that watersheds in the lower basin that were strongly hydrologically altered and presented virtually "flat" hydrographs (i.e., lower-than-expected levels of flow variability; Figure 2c) also hosted fish communities dominated by non-native species (Figure 1c). Overall, our results suggest that increases in flow seasonality would likely (re)introduce beneficial disturbance regimes that increase the persistence of native fishes (Comte et al., 2021; Mims & Olden, 2013; Poff & Zimmerman, 2010) while preventing or slowing down further fish invasions (Kiernan et al., 2012; Marchetti & Moyle, 2001).

4.2.1. Caveats and Future Directions

Our approach is not without caveats, and future research should expand on the proposed spatial network model to tackle additional challenges. First, limitations exist in the datasets used, the most important being the National Inventory of Dams missing smaller structures. Although we captured the main reservoirs and most (>83%) storage in the basin, small dams and weirs can have important cumulative effects on downstream biodiversity—particularly via stream network fragmentation (Bunn & Arthington, 2002; Couto & Olden, 2018) and the disruption of complex organismal life histories (e.g., migration, seasonal floodplain access). Second, slowly-evolving climatic signals may not have been fully captured with the 15 years of flow data used here to maximize spatial coverage. Because directional climate trends should affect controlled and reference watersheds similarly (Ficklin et al., 2018), a longer span of the flow series would likely maintain inferences while also revealing if particular local or contextual factors fluctuate in their relative importance with hydrologic context (e.g., dry years dampening variability at the whole basin scale; wet years allowing dams to have more localized impacts). Third, flow alteration occurs at temporal scales shorter than monthly—particularly downstream of dams that manage flow releases for hydropower production (i.e., hydropeaking) (Bruder et al., 2016). Although ecologically-impactful hydropeaking waves can propagate over tens to hundreds of kilometers (Kennedy et al., 2016; Ruhi et al., 2018), downstream dams often reset such signals. Future research should examine the spatial propagation of these high-frequency alterations to the flow regime. Finally, our focus was on flow regime as a "master variable" of river ecosystem structure and dynamics, but dams also disrupt sediment, thermal, and metabolic regimes, and alteration of these processes may also propagate across the river network (Bernhardt et al., 2018; Olden & Naiman, 2010; Wohl et al., 2015). Actions to mitigate ecological impacts of dams via controlled releases from reservoirs would be more effective if they considered the full suite of links between flow and the biophysical environment, as well as watershed fragmentation impacts that flow management alone cannot solve (Barbarossa et al., 2020; Tharme, 2003).

5. Conclusions

Two and a half decades after the natural flow regime concept was proposed (Poff et al., 1997), environmental flow science is reevaluating the notion of reference hydrologic conditions (Acreman et al., 2014; Poff, 2018): in many cases, return to historical hydrographs is no longer feasible (Milly et al., 2008; Tonkin et al., 2019). This is particularly true in water-scarce regions dominated by multi-year reservoirs like the U.S. West, where large-scale dam decommissioning is unlikely given the need to capture flows in the face of increased climate variability and human water demands (Dettinger et al., 2015; Devineni et al., 2015). Approaches connecting river ecology with engineering can help balance flow-regime integrity with human needs (Poff et al., 2016; Poff & Schmidt, 2016), even if the ecological goal is not to restore the hydrograph to historical conditions but rather to preserve some of its ecologically-significant aspects (e.g., seasonality levels, flood-pulse magnitude, timing of high and low flows) (Yarnell et al., 2015). In this context, understanding which structures and locations in the network are more impactful could help guide the prevention or mitigation of flow alteration impacts more effectively. Given the enormous social and economic capital needed to reoperate large dams (e.g., Minute 319 in the Colorado River), future prioritization efforts could increase realism by considering economic cost of dam reoperation (e.g., in terms of forgone revenue for hydropower), as well as flexibility of the system to accommodate more natural patterns of flow seasonality. Modeling efforts on "designer" flow regimes (Chen & Olden, 2017; Sabo et al., 2017) may be tested and validated via flow release events, which are already frequent even if they could be better leveraged to test hypotheses that advance hydro-ecological science (Olden et al., 2014). Such experiments, combined with an increasing availability of flow and biodiversity time-series data, have great potential to advance the study of flow regime restoration at the river network level, and thus more effective river ecosystem conservation.

Data Availability Statement

Streamflow data were retrieved from the USGS National Water Information System available at https://maps.waterdata.usgs.gov, using the "dataRetrieval" R package (Hirsch & De Cicco, 2015). Naturalized flows were obtained from the United States Bureau of Reclamation Colorado River Basin Natural Flow and Salt Data, available at: https://www.usbr.gov/lc/region/g4000/NaturalFlow/, "Current Natural Flow and Salt Data" tab (https://www.usbr.gov/lc/region/g4000/NaturalFlow/NaturalFlows1906-2019_20210420.xlsx). Dam attributes were retrieved from United States Army Corps of Engineer's National Inventory of Dams database (USACE, 2009) via the "dams" R package (Goteti & Stachelek, 2016). Fish data per HUC8 were obtained at NatureServe (Natureserve, 2018), available at: https://www.natureserve.org/products/digital-distribution-native-us-fishes-watershed; and at the U.S. Geological Survey's Non-indigenous Aquatic Species database (USGS, 2018), available at: https://nas.er.usgs.gov/queries/huc2.aspx/ We excluded records from lentic systems and from non-self-established populations (e.g., eradicated or stocked populations, populations with failed establishment, vagrant species). Species names were harmonized to the species level, according to the Catalog of Fishes (Eschmeyer et al., 2017), and their global conservation status was retrieved from the IUCN Red List (IUCN, 2019).

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