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Indicators of hydro-ecological alteration for the rivers of the United States

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ABSTRACT

Recent decades have produced a river of field data linking hydrologic alteration to fish populations in hundreds of U.S. river systems. Adverse impact thresholds and relationships between flow alteration and fish populations are key for advancing environmental flow conservation and environmental flow regulations in U.S. waterways. Prior work has established relationships in individual rivers and fine scale basins, but not for large basins or at national scale. As a first step toward establishing consistent fish-flow relationships and adverse impact thresholds in every US waterway, we analyze a nation-wide aggregated dataset from McManamay et al., 2017 containing co-located estimates of altered hydrologic metrics (HMs) for flow and native fish richness. In each medium sized river system (HUC4) we (1) identify the hydrologic metrics that most powerfully explain observed impacts on native fish richness, (2) estimate an adverse resource impact threshold defining excessive flow alteration, and (3) attribute the main causes of observed flow alteration. Strong empirical relationships between hydrologic metrics and native fish richness are thus established for most HUC4 basins in the continental U.S., and can be used as guidelines for science-based management. However, the findings underline a major aquatic ecology data gap in the western U.S. where a lack of statistically adequate field observations currently prevent clear results, and this gap will hinder science-based management of those river basins until it is filled.

1. Introduction

Streamflow, or a river's hydrologic discharge, is the ultimate driver of biodiversity and the master variable in fluvial ecological systems (Poff and Ward, 1989; Poff et al., 1997; Richter et al., 1997; Postel and Richter, 2003; Annear et al., 2004). Streamflow determines key aspects of the geomorphological habitat template, sediment transport, nitrogen inputs from the terrestrial catchment, temperature, and species composition both of benthos and in the water column (Leopold et al., 2012; Sparks, 1992; Meixner et al., 2007; Stanford et al., 1996; Bunn and Arthington, 2002; Dewson et al., 2007; Carlisle et al., 2011). Furthermore, streamflow influences organismal abundance, species richness, and food web organization (Seegrist and Gard, 1972; Hemphill and Cooper, 1983; Knight et al., 2014; Sabo et al., 2010; Ruhi et al., 2016; Palmer and Ruhi, 2019). Hence, understanding how alterations from expected – or "natural" – flow regimes adversely impact these aspects of ecological function has become a central pursuit in ecology and the interface between environmental science regulation and management of river ecosystems (Richter et al., 1996, 2003; Postel and Carpenter, 1997; Poff et al., 2010; Peñas et al., 2016; Poff, 2018; Sabo et al., 2018; Fox and Magoulich, 2019; Mims and Olden, 2013).

The impacts of streamflow on ecological function are difficult to directly observe due to intense requirements for hydro-ecological data in all rivers at all scales. Thus, data-driven guidance for co-management of water resources along with aquatic ecosystems is difficult (Poff and Zimmerman, 2010). Furthermore, there are hundreds of streamflow characteristics (referred to here as hydrologic metrics (HMs)) to choose from, and each river has its own relationship between altered HMs and ecological outcomes (Gao et al., 2009; Carlisle et al., 2011). Owing in part to this data gap, environmental policy often neglects key HMs when balancing human and ecosystem requirements for surface water (Postel and Richter, 2003). Here we apply a recently developed national-scale synthesis dataset to develop data-driven indicators of hydro-ecological alteration than can be used for benchmarking river health and setting science-based management targets for each river system, using a consistent methodology.

Managing streamflow starts with understanding the natural flow regime. The natural flow regime is defined as the unique patterns of

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streamflow created from geographic variation in climate, geology, topography, and vegetative cover (Poff et al., 1997). We note that “natural” does not necessarily mean “static” and that an unaltered flow regime would include natural changes in trend, seasonality, and variance (Sabo et al., 2018). Streamflow alteration, or a natural rhythm altered by human activities and the difference between these rhythms, can be quantified by various methods (Richter et al., 1996; Poff et al., 2010; Eng et al., 2013; Carlisle et al., 2010). There are hundreds of correlated HMs to choose from, each one describing a unique characteristic of the natural and altered flow regime (Gao et al., 2009; Eng et al., 2017). Due to this complexity and a lack of data, water resource managers across the U.S. have historically focused on managing for a small and inadequate subset of HMs that may not be appropriate for the local aquatic ecology (Annear et al., 2004; Arthington et al., 2006; Poff et al., 2007, 2010; Sabo et al., 2017).

Relationships between HMs and ecosystem health are foundational for science-based river management policies that include environmental allocation of water, dam operation, flow management, and water use (Poff et al., 2010; Poff and Zimmerman, 2010; Carlisle et al., 2011; Chen and Olden, 2018; Poff, 2018). For example, the State of Michigan constructed empirical relationships between summer base flow and fish species richness for most state streams (Zorn et al., 2012). The relationships identified a threshold of summer base flow alteration that, when exceeded, creates an adverse resource impact (ARI) on the aquatic ecosystem in that river, as indicated by fish species impacts. These ARI thresholds are used to regulate environmental flows by limiting where new large water use permits are issued, to prevent the ARI from occurring. This is a forward-thinking, progressive framework for protecting rivers, but it has not been applicable in many states and river systems owing in part to a lack of data with which to determine the ARI threshold (Poff and Zimmerman, 2010; Knight et al., 2014; Carlisle et al., 2017; Sabo et al., 2017; McManamay et al., 2017). To replicate this model nationwide, data-driven indicators of hydro-ecological alteration are necessary in all rivers at all scales.

When identifying flow-ecology relationships, it is daunting to choose from the hundreds of altered HMs that describe the natural flow regime (Henriksen et al., 2006; Olden and Poff, 2003; Eng et al., 2017). However, not all metrics are necessary in all places and scales (Richter et al., 1996; Gao et al., 2009; Carlisle et al., 2017). Flow metrics are identified based on five fundamental characteristics of the streamflow regime: magnitude, timing, frequency, duration, and rate of change of flow (Richter et al., 1996). There is general agreement among ecologists that flow regime should be the management target, where all five characteristics of the natural flow regime are considered (Annear et al., 2004; Arthington et al., 2006). Here we pay respect to the holistic regime focus by evaluating HMs from all five categories, before determining which characteristics best relate HMs to aquatic ecological health in each continental United States (CONUS) river system. We accomplish this at medium river system scales, using hydrologic unit code 4-digit (HUC4) watersheds, for the single and simple ecological outcome of maintaining native fish richness. Finer-scale analysis and other ecological outcomes are left for future work. The medium-scale results we develop herein can be used for every US river system, and are an effective backstop for water resource managers, regulators, and ecologists to use in the absence of more precise and complete local information.

There are several barriers to developing flow-ecology relationships between flow alteration and ecosystem health on a national scale. First and most critically, a complete data source representing ecosystem health was only recently available (McManamay et al., 2017). Second, methods for creating generalizable functions between streamflow alteration and ecosystem health must be statistically fitted to each geography and scale, with the effects of flow alteration separated from the effects of scale. Third, there is a proliferation of HMs to consider for each river (Carlisle et al., 2017; Eng et al., 2017). To address the data deficiency, we use native fish richness data that are greatly improved by the work of Troia and McManamay (2016) and we use flow alteration data reconstructed using random forest (RF) models by McManamay et al. (2017). We use a statistical model to identify the most relevant HMs in each river system and develop flow-ecology relations for each river system. In the process of establishing relationships in every US river system at the HUC4 scale, we answer three specific research questions: (1) What HMs most strongly control aquatic ecosystem health in each CONUS river system? (2) What are the ARI thresholds in each CONUS river system, and in what rivers can we robustly define ARI thresholds using data that exists today? and (3) To what causes, human or hydroclimate, can we attribute regionally relevant HMs?

2. Methods

2.1. Hydrologic and ecological data

Metrics for hydrologic alteration in NHDplus V1 stream reaches (USEPA and USGS, 2005) were calculated using methods described in McManamay et al. (2017). Flow alteration values and accompanying ARI thresholds do not reflect positive or negative changes in flow, instead they reflect a simplified movement from “natural” or expected flows (McManamay et al., 2017). Hydrologic alteration metrics were calculated for > 7,000 non-reference US Geological Survey (USGS) stream gages by comparing observed (O) conditions to expected (E) natural flow conditions, which were derived from predictive models (McManamay et al., 2017). A total of 43 different hydrologic alteration metrics (Table 1, SI Results WebTable 1) were previously used by multiple studies assessing flow alteration (McManamay et al., 2012, 2014; McManamay, 2014), as these indicators adequately represent the dimensions of flow regimes (Olden and Poff, 2003). We selected these 43 indices because of their utility in sufficiently describing nationwide and regional patterns in hydrologic alteration (McManamay, 2014; McManamay et al., 2012). McManamay et al. (2017) developed a random forest (RF) model to predict hydrologic alteration metrics from a suite of human-disturbance variables (e.g., urban land, agricultural land, dam storage, thermoelectric water usage, etc.). Taking human-disturbance variables for every stream in the nation, McManamay et al. (2017) applied estimates of hydrologic alteration to all NHDPlus V1 stream reaches across the U.S. Lastly, we took mean annual flow at each data point from NHDplusV1 (2006) to calculate the size of the stream reach.

We partitioned native fish richness data into two categories: reach-level (fine scale) and basin-level (coarse scale). At the reach-level, site-specific fish community survey data collected using standardized methodology by US Federal agencies were previously compiled by Troia and McManamay (2016) and spatially joined to NHDPlus V1 stream reaches. Sources of data included Environmental Monitoring and Assessment Program (EMAP), Regional Environmental Monitoring and Assessment Program (REMAP), National Rivers and Streams Assessment (NRSA), and USGS National Water Quality Assessment (NAWQA). These sites represent both reference and non-reference conditions falling across a large range of hydrologic alteration values. This provides a robust richness measure for the entire fish community at reference and non-reference sites, thereby providing a comprehensive data source for examining ecological responses to hydrologic alteration. However, reach-specific data for large river systems were either unavailable or, if data were available, it was not representative of reference conditions. Because reference conditions for large rivers was essentially absent from our dataset, we used basin-level fish data to approximate reference conditions in those systems.

Basin-level fish data were available from NatureServe (2010), which contains an inventory of fish species for HUC8 watersheds in the US. However, one cannot assume that all the listed species occurring in an entire HUC8 basin will occur within a specific stream reach. Therefore, we identified the NHDplusV1 stream reaches at the outlet of each HUC8 basin as each basin’s pour point. Using information on habitat

Table 1
Hydrologic metric codes and names organized into six streamflow regime categories. See *SI Results* WebTable 1 for additional information on hydrologic metric definitions.

Code	Definition
Magnitude of flow events	
MA1	Mean Daily Flow
MA2	Median Daily flow
MA3	Variability in daily flows
MA12-23	Mean monthly flow for all months, January (12) through December (23)
MA41	Mean annual runoff
ML17	Baseflow 1. Seven-day minimum flow divided by mean annual daily flows averaged across all years.
ML19	Baseflow 2. Mean of ratio of the lowest annual daily flow to the mean annual daily flow times 100 averaged across all years
MH20	Mean annual maximum flows divided by catchment area
Duration of flow events	
DL1-5	Magnitude of minimum annual flow for 1-/3-/7-/30-/90-day means
DL16	Low flow pulse duration
DL18	Number of zero-flow days
DH1-5	Annual maxima of 1-/3-/7-/30-/90-day means of daily discharge
DH15	High flow pulse duration
Frequency of flow events	
FL1	Low flood pulse count. Number of annual occurrences during which the magnitude of flow remains below a lower threshold.
FH1	High flood pulse count. See FL1.
FH6	Flood frequency. Mean number of high flow events per year using 3 times median annual flow
FH7	Flood frequency. Mean number of high flow events per year using 7 times median annual flow
Timing of Flow Events	
TA1	Constancy
TA2	Predictability of flow
Rate of Change of flow events	
RA1	Rise rate. Mean rate of positive changes in flow from one day to the next.
RA3	Fall Rate. Mean rate of negative changes in flow from one day to next.
RA8	Reversals. Number of positive and negative changes in water conditions from one day to the next.
Other	
HA_Rank	Cumulative hydrologic alteration. See McManamay (2017)
Seasonal	Seasonality alteration. See McManamay (2017).

preference (Frimpong and Angermeier, 2009), we then identified fish within each HUC8 that prefer medium streams to larger systems (i.e., avoiding species solely occurring in headwaters or creeks). This joining of data rendered a subset list of species likely to occur at the pour point. After all data were compiled, a total of 6452 stream reach locations with overlapping hydrologic and ecological data were created with alteration values between zero and one for 43 different hydrologic metrics (Table 1, SI Results Table 1).

2.2. Regional stratification

Understanding native fish richness patterns requires accounting for regional differences influencing the biogeography of fish species. We organized CONUS stream reaches into 29 ecohydrologic regions, as well as their associated HUC4 watersheds. Ecohydrologic regions represent a spatially unique combination of freshwater ecoregions (Abell et al., 2008) and HUC2 watersheds. Freshwater ecoregions are based on the distribution and composition of freshwater fish species incorporating major ecological and evolutionary patterns (Abell et al., 2008). All statistical analyses were conducted on the HUC4 scale and results were aggregated to the appropriate ecohydrologic region.

2.3. Statistical analysis

Species richness and hydrologic alteration data often create difficult to interpret relationships (Cade and Noon, 2003; Knight et al., 2014; Poff and Zimmerman, 2010). The reasons being are the multiple limiting factors in a stream network that affect native fish richness, therefore, testing a single limiting factor, such as streamflow, against richness will create a weak relationship between the predictive factor (x) and the response variable (y) (Cade and Noon, 2003). Yet the data uncertainty does not suggest a relationship is absent. Standard linear regression is not capable of identifying these relationships (Cade et al., 1999). More recently, ecologists have used quantile regression to identify relationships between a single predictive factor, when many exist, and the response variable (Cade and Noon, 2003; Cade et al., 1999). Quantile regression identifies and quantifies upper and/or lower bounds of “wedge-shaped point distributions” and, by extension, the limiting influence of an explanatory variable to a response variable (Knight et al., 2008; Konrad et al., 2008). In other words, it offers the flexibility of exploring multiple rates of change for different quantities of the distribution, giving a more complete picture of the relationship between variables missed by other regression methods (Cade and Noon, 2003). Due to the multiple limiting factors within a stream network, we use quantile regression as the method for identifying relationships between altered HMs and native fish richness for all CONUS HUC4 watersheds (SI Methods, SI Results WebFigure 1).

2.4. Hydrologic drivers of indicators of alteration

To quantify the relationship between hydrology (natural and human-modified) and regionally important indicators of human alterations to natural hydrology, we constructed a choice model with six macroscale hydrologic variables as continuous predictor variables of the top indicator (highest r-squared) which in turn is a multivariate categorical, response surface (SI Methods). Predictor variables included: 1) contributing area, 2) average annual runoff for the period 1950–1999 (summed across the HUC 4 as estimated by the VIC model) (Sabo et al., 2010), 3) total annual withdrawals (based on 2005 data from USGS water use survey), 4) reservoir storage standardized by total annual runoff (Sabo et al., 2010), dam density (dams per km2 of wetted river channel, from Sabo et al., 2010) and a water stress index (total annual withdrawals standardized by average annual runoff’; sensu Oki and Kanae, 2006). The choice model is set up like a logit-regression where the dependent variable or “choice” is the most highly supported HM (by r^2 from quantile regression) and the independent variables are the macroscale hydrologic predictors listed above.

We used a multi-model inference approach (Burnham and Anderson, 2002, SI Methods) to identify predictor variables and models (comprising different subsets of predictors) with the most support. We fitted models for all possible subsets (combinations) of the six fixed effects and then compared relative support using calculated model importance using the difference between model AIC and minimum model AIC, or: $\Delta AIC = AIC_i - \min AIC$. The model with the most support has $\Delta AIC = 0$. We considered models to have good support with ΔAIC values less than 10. The USGS cataloguing units (HUC4) were the unit of replication, but we estimated separate intercepts for each USGS hydrologic region (HUC 2). The analysis was conducted in R version 3.4.4 using the multiform function in the nnet package.

3. Results

3.1. Flow-ecology relationships

Initial examination of the dataset found an average of 21 reach-level fish data points and 10 basin-level fish data points in each HUC4 with fish data, each located along a specific river reach. HUC4s contained reach-level fish data sample sizes ranging from 3 to 200 data points per catchment. Twelve percent of HUC4 watersheds mostly occurring in the Western U.S. were unusable at the start of the analysis due to too few reach-level data points (2 or less). Hence, we used a total of 180 qualified HUC4s to analyze relationships between HMs and native fish richness. See SI Results WebFigure 2 for a map of overlapping hydrologic and ecological data points included in the original dataset.

The quantile regression revealed flow-ecology relationships in watersheds across CONUS, conditional to the quantile being examined. Sixty-three percent of CONUS HUC4 basins contained a statistically significant relationship between an altered HM and native fish richness residuals in qualified basins using the upper-most 95th quantile (Table 2). For each HUC4 watershed with a significant flow-ecology relationship we identified a most strongly explanatory hydrologic metric and an ARI threshold based on this metric (SI Methods, SI Results WebTable 2). The number of statistically significant relationships decreased for lower quantiles (Table 2). A decrease in slope in the modeled line is observed as we move from higher quantiles to lower quantiles, indicating that other unmeasured limiting factors are impacting native fish richness. This phenomenon is common in studies examining species count data where all possible factors affecting ecological processes, such as nutrient concentrations, water temperature, and habitat availability, are not measured (Cade and Noon, 2003; Knight et al., 2008). Fig. 1 shows two basin-specific relationships, revealing an interpretation of flow alteration at the upper bounds (75th, 85th, and 95th) and ARI thresholds identified for each quantile line. The 95th quantile line in HUC 0109 indicates for a given river in said basin that contains zero level of flow alteration (x), we can say with 95% probably changes in native fish richness will equal y. Furthermore, for river policy and management, a level of concern will occur at $x = 0.39$ when using the 95th quantile because at this value native fish richness is likely to decline. The value of these relationships lies in their ability to indicate favorable or unfavorable conditions for native fish richness with a quantified level of certainty.

The flow-ecology relationships displayed a diversity of most important HMs in basins across CONUS (Fig. 2). Of the 105 HUC4 watersheds with passing metrics at the 95th quantile, low flow metrics were found to be the best-fit metrics in 20% of HUC4s, high flow metrics in 20%, and average flow metrics in 53%. Magnitude metrics were represented in 43% of HUC4s and duration metrics in 21%. Frequency metrics were in 14% HUC4s, rate of change metrics in 10%, and timing metrics in 4%, and other in 7%. Fig. 2 illustrates HUC4s with their most important (highest r^2) metrics and associated ecohydrologic regions. Overall, the eastern U.S. has far greater results than the western U.S. For the East, the model worked best in the Northeast and Midwest regions. The southwestern U.S. and Snake River-Columbia basins had the lowest number of returning metrics. See SI Results WebTable 2 for a list of most significant non-abbreviated metrics in each HUC4 watershed, and their associated ARI threshold at the 95th quantile.

Spatial patterns for flow conditions (low, average, and high) and categories (magnitude, duration, timing, etc.) of high-ranking metrics were apparent in different regions of the country (Fig. 2). For example, the Northeast ecohydrologic region contained 75% average flow condition metrics and 75% are within the magnitude category (Fig. 2). These results indicate that average flow condition metrics within the magnitude category have a greater effect on native fish richness than other metrics for the Northeast ecohydrologic region. The Tennessee ecohydrologic region returned only magnitude metrics with average flow conditions, yet, all four metrics were different (MA15, MA16, MA18, MA41). Lastly, the Lower Colorado East ecohydrologic region produced only low flow duration metrics for 40% of its nested HUC4s. These spatial patterns may provide insight on the prioritization of metrics in certain regions of the country.

ARI thresholds varied considerably for CONUS HUC4 basins at the 95th quantile (Fig. 3). Values for thresholds ranged from 0.08% to 95%. The mean threshold value for all significant metrics was 38% alteration with a standard deviation of 20%. We see clusters of “less sensitive” thresholds (57%-95% alteration required) in the Mid Atlantic South, Mid Atlantic North, and Northeast ecohydrologic regions, but more sensitive thresholds of 1% to 23% in the Midwest U.S, specifically in our Upper Mississippi, Lower Mississippi East, and Upper White ecohydrologic regions.

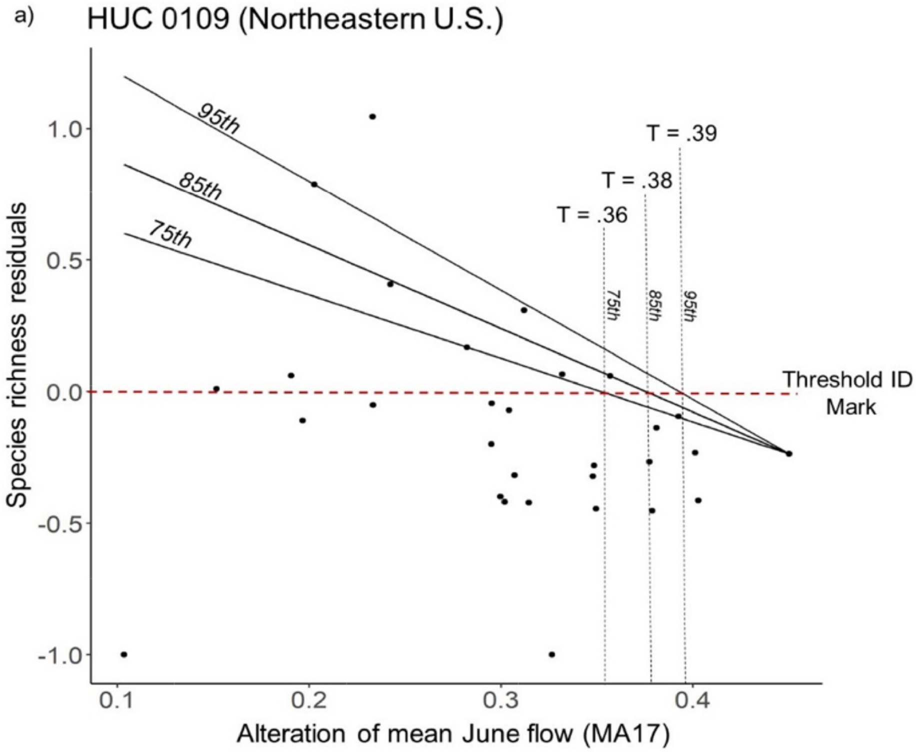
Although results were statistically significant for most regions of the country, three ecohydrologic regions (California North, California Central, California South) in the western U.S. did not render any HUC4s with a significant flow-ecology relationship or robust ARI threshold. Additionally, some HUC4s produced statistically significant results (p-value < 0.10) that did not align with our criteria for interpretable flow-ecology relationships (SI Methods). Thirty two percent of statistically significant metrics had a positive flow-ecology relationship at the 95th quantile. At least one positive flow-ecology relationship was found in 74 of 180 HUC4s. The HUC4 with the largest number of passing metrics ($n = 34$) with this positive slope was HUC 0806 located within the Lower Mississippi ecohydrologic region. Overall, approximately 12% of qualified HUC4s in CONUS had zero metrics meeting our criteria when using the 95th quantile.

3.2. Hydrologic drivers of indicators of alteration

We present relationships between hydrology, human alterations to local hydrology, and indicators of alteration. Coefficients from the full model were non-zero and significant for all six predictor variables except contributing area (Table 3, SI Results WebTable 3). Multi-model inference revealed the model with the most support was one with a single predictor—dam density—and this model garnered 96% of the AIC weight. Two other single parameter models also had reasonable support ($\Delta AIC < 10$), one including withdrawals (2.1% of the weight) and the other including only reservoir storage (1.6% of the weight). Hence the density of dams in the HUC4 appears to be the strongest

Table 2
Statistically significant relationships between flow alteration and species richness exist in the upper quantiles for HUC4 watersheds, with a decrease in statistically significant flow-ecology relationships as the quantile is lowered.

Quantile	Unique Significant Metrics		HUC4 Coverage		Ecohydrologic Region Coverage	
0.95	32	74%	114	63%	26	89%
0.90	33	77%	103	57%	26	89%
0.85	31	72%	96	53%	26	89%
0.80	32	74%	86	47%	24	83%



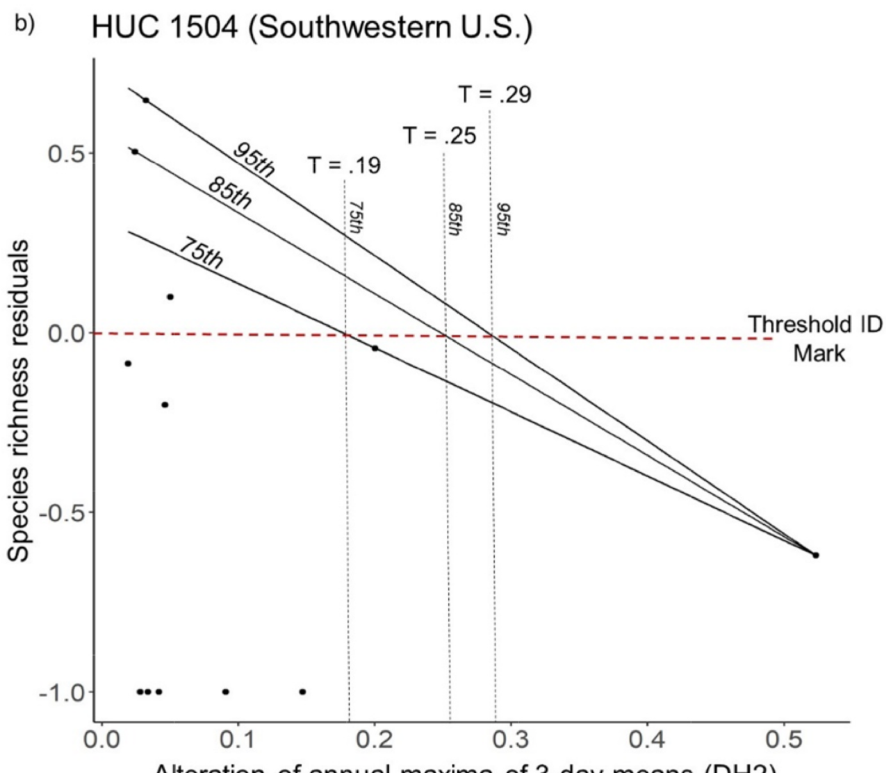


Fig. 1. An example of flow-ecology relationships for two HUC4 watersheds show a negative relationship exists between flow alteration of labeled hydrologic metric and species richness residuals for upper quantiles, with a varying rate depending on sample size, location, and quantile used. ARI thresholds for each quantile line are labeled with “T”. See *SI Results* WebTable 2 for best metrics and ARI thresholds in all qualified HUC4 watersheds using the 95th quantile.

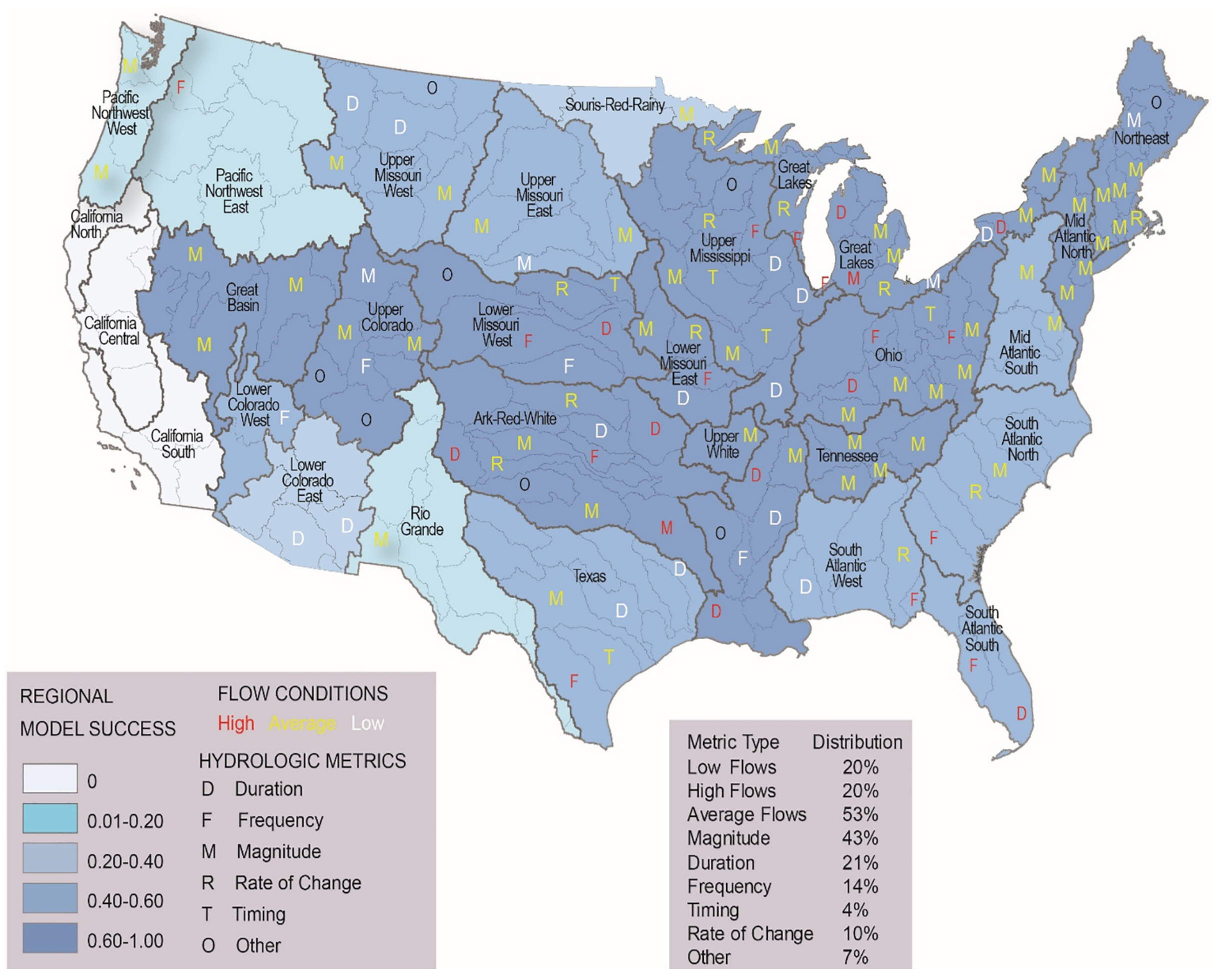


Fig. 2. Single best-fit metrics for HUC4 watersheds and their corresponding ecohydrologic region. Regional model success for ecohydrologic regions (percent of nested HUC4 watersheds with significant flow-ecology relationship) is denoted by shades of blue. Letters represent metric type while color denotes flow condition. Metric letters are placed inside corresponding HUC4 watersheds.

predictor of the flow alteration indicator most strongly related to native fish richness across CONUS.

4. Discussion

Below we interpret these findings for the purpose of application and discuss the limitations of our findings. The quality of the flow-ecology relationships met statistical criteria of quality for 63% of the 180 qualified CONUS basins when using the 95th quantile criterion. Hence, streamflow characteristics are clearly a major factor in aquatic ecosystem health in U.S. rivers. This result demonstrates that generalized functions relating streamflow characteristics to ecosystem health can now be determined in most US river systems using currently available data. Scientifically defensible regional streamflow rules and adverse resource impact (ARI) thresholds that balance both human and ecosystem requirements for water can now be established in most parts of the US using these results, even where detailed local field studies are unavailable or inadequate. The exception to this finding is the western and southwestern US, where the absence of reach-level native fish richness data prevented the establishment of robust regional flow-ecology relationships. These results should motivate action, specifically (1) the adoption of science-based and regionally-specific ARI thresholds and regulations for all US rivers by both State and Federal environmental agencies, and (2) the collection of more complete fish species data especially in western US river systems to fill the lingering data gap. Flow-ecology relationships have been quantified in this manner before (Zorn et al., 2012; Knight et al., 2014), but never with a nation-wide scope.

Our analysis suggests dam density alone is the strongest predictor of which flow alteration indicators are most strongly related to native fish richness in a river system; total water storage is also a major predictor. Dam density is inversely related to longitudinal habitat connectivity in the river system, impeding species dispersal and upstream migrations of anadromous and catadromous fishes (Johnson et al., 2008; Poff et al., 2007; Grill et al., 2019; Ziv et al., 2012). The importance of dam density is not surprising given previous work, but the observation that it supersedes storage or withdrawal as a determinant of streamflow and aquatic ecosystem alteration across CONUS- even when standardized by total runoff- is noteworthy.

We suspect dam density impacts alteration by at least three mechanisms. First is the likely disruption to the river network connectivity —precluding dispersal and increasing local extinctions. Second is the likely increase in river continuity, because dams homogenize flow conditions (Stanford and Ward, 1983) and fauna (Poff et al., 2007) and by extension, higher numbers of dams in a drainage increase homogeneity of fauna and their habitat at the regional HUC4 scale. Finally, cascades of dams in river networks likely impact compounding alterations on variation in discharge, and this variation is a strong predictor of spatial patterns in fish production (Sabo et al., 2017) and biodiversity (Ruhi et al., 2016).

We recognize there are other factors that could influence biodiversity other than our HMs (Oberdoff et al., 1995). However, quantile

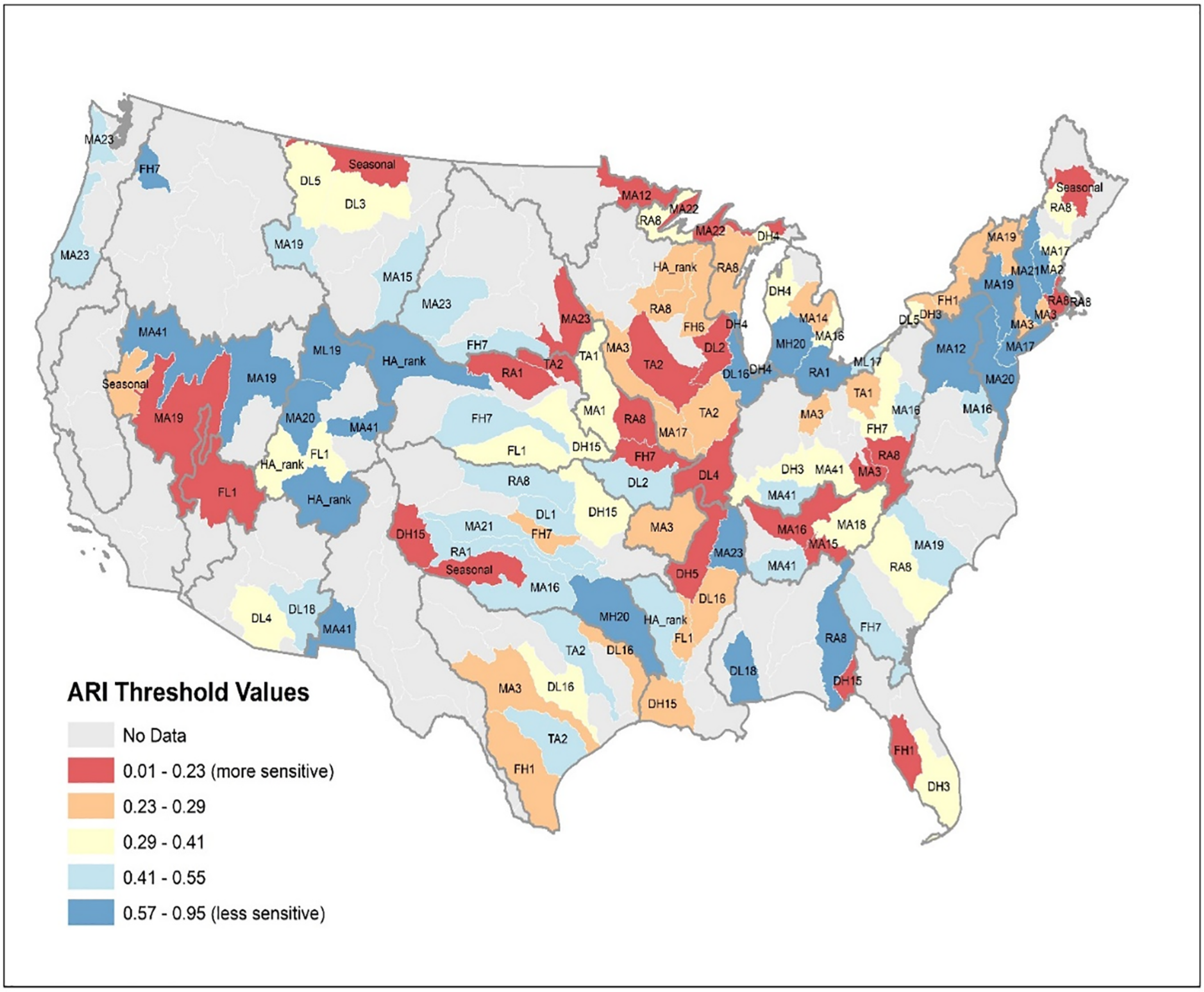


Fig. 3. Full metric code names and accompanying ARI threshold values for CONUS HUC4 basins. See Table 1 for hydrologic metric code definitions.

Table 3
Model importance via multi-model inference for hydrologic drivers of indicators of alteration.

Model	Predictors	AIC	K	del AIC	AIC Weight
1	Dam Density	1159.511	20	0	0.96
2	Withdrawals	1167.217	20	7.705175	0.02
3	Reservoir Storage	1167.738	20	8.226317	0.02

regression provides an approach to consider the "limiting factor" and confidence levels associated with those limits (Knight et al., 2014). As such, this approach is well suited for the relationships suggested within the Ecological Limits of Hydrologic Alteration framework (Poff et al., 2010). This threshold type approach is robust in that it presents a degree of confidence that hydrologic alteration beyond a given threshold will induce ecological impact. It is likely that systems will experience impacts well within those thresholds given changes to temperature and water quality – however, that is beyond the scope of our analysis.

Even when using this new synthesis dataset, many rivers' flow-ecology relationships consisted of small sample sizes and marginal statistical relationships. These small sample sizes are due to a lack of reach-level fish species data. This data limitation correspondingly constrains spatial overlap between hydrologic and ecological data within a HUC4 watershed, therefore limiting significant quantile slopes to upper quantiles only (Carlisle et al., 2011; Knight et al., 2014). Spatial overlap is largely nonexistent for finer spatial scales, rendering the statistics unworkable using current data. In addition, the wedge-shaped scatter plot relationship between the altered HM and native fish richness suggests the existence of multiple co-limiting factors within the ecosystem. For water managers and policy, this situation can be problematic. For water policy, interpreting flow-ecology relationships with only the upper 75th, 85th, and 95th quantiles and not smaller quantiles limits the scope of application of our findings (Knight et al., 2014). Hence, these relationships are most applicable for regional streamflow management, and it is unknown at present how applicable the results may be for management of a specific river reach at a finer scale.

5. Conclusion

Empirically accurate indicators of hydrologic alteration for all rivers and at all scales significantly improves our ability to effectively and accurately manage aquatic ecosystem health (Poff et al., 2010; Knight et al., 2014; Sabo et al., 2017). Prior efforts to establish these indicators have been held back by gaps in both scale and geography of field studies (Poff and Zimmerman, 2010; Knight et al., 2014). Here we redress these gaps using a recently published synthesis dataset for CONUS HUC4 scale river systems (Troia and McManamay, 2016). We calculated best-fit metrics from said relationships that show how the strongest HMs for aquatic ecosystem health vary regionally, therefore stressing the importance of regionalized metrics for water resource managers and state water policy. For each best-fit metric an ARI threshold was identified, indicating a level of flow alteration likely to adversely impact aquatic ecosystem health (Zorn et al., 2012). Lastly, we identified the driving factors to which we can attribute regionally important altered metrics; dam density, water withdrawals, and total storage are the leading factors nationwide. However, a gap in the completeness of data remains for many western U.S. river systems and for river scales finer than HUC4.

This gap in completeness is likely a result of two major limitations. First, these findings consider a wide variety of HMs, but are limited to a single simple indicator of aquatic ecosystem health- native fish richness. Second, low sample sizes of native fish richness in regions of the country such as the western U.S. create estimates of high uncertainty. Future studies should build on this work by examining other regionally specific limiting factors, such as macroinvertebrates, and/or attempting to build a more geographically comprehensive dataset on native fish richness. For the latter to be possible, state and federal agencies must create accessible and comprehensive databases on native fish richness for all waterways. We recommend relying on more field-based richness data across all types of rivers with varying degrees alteration. As a result, water managers can develop flow-ecology relationships between HM's and native fish richness for a wider spatial scale, further refining ecologically responsible ARI thresholds for water resource management.

All authors contributed to the writing. George led the writing and the analysis of the data. McManamay provided data and analysis along with foundational ideas. Perry performed spatial analysis and mapping. Ruddell led the project as PI and provided foundational ideas. Sabo is Co-PI and performed attribution analysis along with foundational ideas.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106908.

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