Patterns and drivers of fish extirpations in rivers of the American Southwest and Southeast

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Abstract
Effective conservation of freshwater biodiversity requires spatially explicit investigations of how dams and hydroclimatic alterations among climate regions may interact to drive species to extinction. We investigated how dams and hydroclimatic alterations interact with species ecological and life history traits to influence past extirpation probabilities of native freshwater fishes in the Upper and Lower Colorado River (CR), Alabama-Coosa-Tallapoosa (ACT), and Apalachicola-Chattahoochee-Flint (ACF) basins. Using long-term discharge data for continuously gaged streams and rivers, we quantified streamflow anomalies (i.e., departure “expected” streamflow) at the sub-basin scale over the past half-century. Next, we related extirpation probabilities of native fishes in both regions to streamflow anomalies, river basin characteristics, species traits, and non-native species richness using binomial logistic regression. Sub-basin extirpations in the Southwest (n = 95 Upper CR, n = 130 Lower CR) were highest in lowland mainstem rivers impacted by large dams and in desert springs. Dammed flow seasonality, increased longevity (i.e., delayed reproduction), and decreased fish egg sizes (i.e., lower parental care) were related to elevated fish extirpation probability in the Southwest. Sub-basin extirpations in the Southeast (ACT n = 46, ACF n = 22) were most prevalent in upland rivers, with flow dependency, greater age and length at maturity, isolation by dams, and greater distance upstream. Our results confirm that dams are an overriding driver of native fish species losses, irrespective of basin-wide differences in native or non-native species richness. Dams and hydrologic alterations interact with species traits to influence community disassembly, and very high extirpation risks in the Southeast are due to interactions between high dam density and species restricted ranges. Given global surges in dam building and retrofitting, increased extirpation risks should be expected unless management strategies that balance flow regulation with ecological outcomes are widely implemented.

KEYWORDS
biodiversity loss, dams, flow regime, global change, imperiled species
Climate-induced changes in freshwater environments interact with hydrologic alterations by dams to affect the persistence of aquatic life (Vörösmarty et al., 2010). Worldwide presence of dams has dramatically impacted riverine flow regimes (McManamay, Orth, & Dolloff, 2012; Poff, Olden, Merritt, & Pepin, 2007), fundamentally altering physical habitat and putting at risk numerous threatened and endangered fish species (Dudgeon et al., 2006; Freeman, Irwin, Burkhead, Freeman, & Bart, 2005; Jeik et al., 2008; Vörösmarty et al., 2010). Both flow quantity and variability (i.e., the characteristic magnitudes, frequencies, and timings of seasonal high and low flows) are critical for supporting ecological integrity in rivers (Poff et al., 1997). However, the habitats of regulated rivers are often disconnected both laterally and longitudinally, and many of the flow regime features that shaped morphological, behavioral, and life history adaptations of biota, are dampened or lost through complex interactions between hydroclimatic changes and dams (Bunn & Arthington, 2002; Olden, 2016; Rolls, Leigh, & Sheldon, 2012).

Conservation efforts in flow-regulated rivers have attempted to balance water needs for both humans and threatened plant and animal species (Arthington, 2012; Olden et al., 2014). Achieving this goal is challenging because over-allocation of freshwater resources continues to drive water scarcity, threatening both water security and freshwater biodiversity (Dudgeon et al., 2006; Vörösmarty et al., 2010). In the American Southwest, surface and groundwater resources are increasingly used by humans, often at the expense of native species (Sabo et al., 2010). Human demands for fresh water, coupled with climate-driven increases in regional water scarcity (Seager et al., 2007, 2013), will further alter both extreme low- and high-flow events, threatening native fish communities and favoring invasion by non-native species (Jaeger, Olden, & Pelland, 2014; Ruh, Olden, & Sabo, 2016). Similarly, high dam densities in the American Southeast have restricted the ranges of native fishes, leading to reductions in population size and geographic range of imperiled fauna (Freeman et al., 2005; Sabo et al., 2010).

Mounting evidence suggests that environmental change is the cause of biologic communities being disassembled (i.e., altered) according to spatially and temporally heterogeneous rates of species losses (Zavaleta et al., 2009). Changes in species composition, rather than systematic reductions in species richness, appear more common (Dornelas et al., 2014), and regions with high biodiversity may support the persistence of threatened species (Weeks, Gregory, & Naeem, 2016). Traits-based approaches have proven powerful for understanding species-specific reductions in native and increases in non-native species ranges (Olden, Poff, & Bestgen, 2006), and responses to changing riverine conditions, including alterations in flow regimes (Mims & Olden, 2013) and land use practices (Moore & Olden, 2017). This information, coupled with spatially explicit quantification of flow and hydroclimatic alteration in different climate regions, is needed to predict impending extinctions and better conserve threatened species in regulated river networks.
A total of 79 gages met these criteria for the Upper (n = 58 sub-basins) and Lower CR (n = 65 sub-basins), 14 gages for the ACF (n = 12 sub-basins), and 6 gages for the ACT (n = 14 sub-basins). For sub-basins lacking a gage, we selected the nearest downstream gage to represent discharge within that sub-basin, and mean discharge was used for sub-basins (i.e., ACF) with multiple gages. Daily
discharge (measured as liters per second from USGS data) was estimated for each sub-basin based on data from the nearest downstream gage. The Discrete Fast Fourier Transform (DFFT) allowed parsing out seasonal from interannual variation in discharge, and resulting departures from “expected” streamflow or streamflow anomalies (after Sabo & Post, 2008), to obtain metrics of interest (described below). The DFFT routine was performed on mean daily discharge data at the selected gages, using the discharge package (https://sourceforge.net/projects/discharge/) in R (R Development Core Team, 2015). After running DFFT, we first extracted signal-to-noise ratios (hereafter SNR), a ratio between seasonal and interannual variation in daily discharge (with both elements being measured as a root mean squared amplitude, delivering a unitless ratio expressed on a decibel scale). SNRs are ecologically meaningful because they represent a measure of the relation between predictable, seasonal flow patterns (i.e., those that have driven organismal adaptations) relative to stochastic flow variability (i.e., ecological disturbances) (Sabo & Post, 2008). Second, we estimated “catastrophic” flow variation based on the distribution of positive (high-flow) and negative (low-flow) residuals (after Sabo & Post, 2008). Extreme low ($\sigma_{nl}$) and high streamflow intensities ($\sigma_{nh}$) reflect the standard deviation of residual discharge events, and thus quantify how common are extreme residual flows compared to small deviations from the seasonal trend. See Supporting Information for all streamflow covariates from each basin (Table S1), which includes additional covariates which we did not relate to extinction probabilities (see below).

2.2 River basin characteristics

To understand the effects of fragmentation by dams on fish extirpation, we computed dam-related metrics at the sub-basin scale. The United States has a rich history of dam construction, with subsequent effects on riverine hydrologic regimes (Graf, 1999). We focused on rivers in the Upper and Lower CR, ACT, and ACF basins to test for effects of altered discharge on extirpation probability among diverse fish communities. A total of 53 large dams exist in the CR (Upper $n = 32$, Lower $n = 21$), 13 in the ACT, and 7 in the ACF. For each sub-basin in the CR, ACT, and ACF river basins, we determined the presence/absence of dams, the distance (km) from the river mouth, and river km impounded by dams using ArcGIS spatial data layers in ArcMAP (version 10.2) Esri, Redlands, CA, USA. See Table S1 for a complete database of streamflow alterations and basin characteristics from individual HUC8 sub-basins for (CR), (ACT), and (ACF) basins.

2.3 Fish species traits

To understand the biologic correlates of native extinction risk, a trait database was developed for all fish species (native and nonnative) known to occur (either in the past or in the present) in the study area. This included a total of 18 species in the Upper CR, 37 species in the Lower CR, 130 species in the ACF and 201 species in the ACT. Ecological traits associated with macrohabitat preference, flow dependence, reproductive strategy, longevity, and maximum body length were derived from multiple sources (Boschung & Mayden, 2004; Goldstein & Meador, 2004; Mims, Olden, Shattuck, & Poff, 2010; Page & Burr, 1991) (see Table S2 for the full trait database). The subset of traits included in the subsequent analyses were as follows: fluvial dependence (reliance on flowing waters for completing life cycle, e.g., flow required for feeding or reproduction [classified as yes or no]), longevity (maximum potential lifespan [years]), length at maturation (cm), age at maturation (years), fecundity (total number of eggs or offspring per breeding season), egg size (mean diameter of mature [fully yolked] ovarian oocytes [mm]), and caudal fin aspect ratio ($A = h^2/s$, $h$ = height of the caudal fin; $s$ = surface area of fin) as a measure of swimming ability. We focused on these life history traits based on previous studies that assessed the importance of geographic range on vulnerability of native fishes to flow alteration (Olden et al., 2006; Rolls & Sterbern, 2012).

2.4 Fish extirpation status

Imperilment status of native fishes was determined from Jelks et al. (2008), and extirpation status was estimated from historical observations, databases (NatureServe, Aquatic GAP, Georgia Museum of Natural History), and expert opinion. Building on a previous effort in the ACT (Freeman et al., 2005), we expanded assessments of individual species imperilment and extirpation status to all sub-basins in the ACT and ACF. A species was considered extirpated if it was not found after repeated surveys for a period of at least 20 years (Freeman et al., 2005). For the CR, detailed pre-1980 fish surveys were lacking, so we determined historical (pre-1980) ranges based on data from NatureServe and present-day (post-1980) ranges from a large compilation of databases that ensured comprehensive coverage of the entire basin (Strecker, Olden, Whittier, & Paukert, 2011; Moore & Olden, 2017; J. Olden, unpublished data). Historical species lists were used as the taxonomic basis for comparing present-day occurrences (if a species is historically absent, extirpation probability cannot be quantified). In addition, we quantified species richness of non-native fishes within each sub-basin as an additional covariate for models of native species extirpation (see below).

2.5 Data analysis

2.5.1 Covariate selection and extirpation probabilities

To discern to what extent differences in flow regimes were due to climate vs. flow regulation, we compared the magnitude of streamflow anomalies from HCDN and non-HCDN gages within each basin (CR, ACT, and ACF) using two sample t-tests and Welch’s test for unequal variance. Due to lack of spatial representativeness throughout entire river basins, we pooled streamflow anomalies from HCDN and non-HCDN basins across sub-basins within each river basin.
We combined data on flow regime characteristics, sub-basin characteristics, and species trait characteristics, to understand the drivers of native fish extirpation probability. To this end, we first tested for multicollinearity among covariates using the variance inflation factor (vifcor function and usdm package in R) (Naimi, et al., 2014). Covariates with high collinearity (>9) were removed (see Table S2 for all covariates), obtaining the following subset of covariates: extreme low- and high-flow intensities, SNR (streamflow anomalies); distance (km) upriver, km impounded, dam isolated (sub-basin characteristics); flow dependence, longevity, length and age at maturity, fecundity, egg size, aspect ratio (species traits); and nonnative species richness within each sub-basin.

We then ran binomial logistic regression models using extirpation probability of each native freshwater fish within a sub-basin as a response, and all covariates plus species identity as explanatory variables. Covariates (n = 14) were treated as fixed effects. Covariates were standardized to z-score to scale measurements and aid interpretation among continuous predictors (Gelman & Hill, 2007). Model selection was based in all possible subsets, and was determined using the bestglm package in R with the information criterion set to cross-validation across various model selection criteria types (McLeod & Xu, 2010). We calculated the percentage (%) difference in odds by subtracting 1 from the odds ratio and multiplying by 100, where the odds ratio is the exponent of the regression coefficient. We calculated % difference in odds of extirpation within each sub-basin for every 1-unit increase in a given quantitative covariate (or presence of a binary covariate). A different model selection procedure was run for each basin (CR, ACT, ACF), thus obtaining basin-specific drivers of native fish extirpation.

3 | RESULTS

3.1 | Hydrologic alterations and historical discharge variance

Climate vs. human controls on streamflow anomalies were significantly different in Southwest but not Southeast rivers. Specifically, climate drivers increased high-flow anomalies and decreased streamflow seasonality in the CR but not in the ACT or ACF (Fig. S1). Spatial patterns in long-term flow anomalies (extreme low- and high-flow intensities from daily discharge measured as liters per second) varied within and among sub-basins of Southwest and Southeast rivers. Differences in extreme low- and high-flow intensities were 3–4 times greater in the CR (Figure 3a,b) than either the ACT or ACF (Figure 4a,b). The greatest high-flow intensities were estimated in lowland basins of the Lower CR (Figure 3b), which are directly influenced by seasonal monsoonal storms. Extreme low- and high-flow intensities in the Southeast were 2 times greater in Piedmont and Coastal Plain than upland rivers of both the ACT and ACF (Figure 4a,b). The Upper CR sub-basins were characterized by high SNRs relative to Lower CR sub-basins; these differences are explained in part by higher contributions of seasonal snowmelt to daily discharge in the Upper CR (Figure 4c).

3.2 | Trait correlates of fish extirpation

A total of 37 native species was recorded in the Lower CR and 18 in the Upper CR (Figure 5a). Sub-basin species richness was more heterogeneous in the Lower CR basin than the Upper CR basin, with generally higher richness within a given sub-basin for the Upper CR. In the CR, combinations of species-watershed extirpations (n = 95 Upper CR, n = 130 Lower CR) have been highest among large-bodied, migratory, and endemic fishes (e.g., cutthroat trout, bonytail chub, humpback chub) in lowland mainstem rivers directly impacted by large dams, as well as a number of spring-dwelling fishes (Figure 5a). Extirpation probabilities were greatest for endemic, fluvial-dependent fishes in mainstem rivers of the Southwest and endemic headwater fishes restricted by dams in the Southeast (Table 1). Flow SNR, longevity and egg size were highly correlated with the probability of extirpation in the CR. Declines in SNR (decreasing seasonality in streamflow) as well as smaller egg size (denoting low parental care to offspring) were related to increased extirpation probability by 36% and 24%, respectively. Longer lifespan increased extirpation probability by 65% (Table 1). Despite high non-native species richness in many sub-basins throughout the CR (Table S1), this covariate was not a predictor of past native species extirpation risk at the spatial grain examined here.

A total of 201 native species was recorded in the ACT and 130 in the ACF (Figure 5b). Sub-basin species richness was higher and more heterogeneous in the ACT than the ACF. Combinations of species-watershed extirpations in the ACT (n = 46) have occurred largely in upland sub-basins involving small-bodied endemic species (e.g., darters), and migratory and large-bodied fishes (e.g., sturgeon, shad, pike, eel), and combinations of species-watershed extirpations in the ACF (n = 22) have occurred in upland sub-basins for migratory and large-bodies fishes (e.g., sturgeon, shad, eel; Figure 5b). In the ACT, distance from river mouth (km upstream), flow dependence, age and maximum length at maturity, fecundity, longevity, and egg size were all important covariates explaining extirpations (Table 1). Distance from river mouth increased extirpation probability by 101%, and dependence on flow had greatly increased extinction risk (Table 1). Higher age and maximum length at maturity both greatly increased probability of being extirpated, whereas lower fecundity, lower longevity, and smaller egg size were associated with higher extirpation risk (Table 1). In the ACF, distance from river mouth, dam isolation, age at maturity, longevity, and fecundity were covariates explaining extirpations (Table 1). Fish that were isolated upstream by dams, had higher age at maturity, or higher fecundity were predicted to have higher extirpation probabilities, whereas long-lived fishes had a 100% decreased probability of being extirpated (Table 1). Non-native species richness was low among sub-basins of the ACT and ACF (Table S1) and was not a predictor of past native species extirpation risk in either basin.

4 | DISCUSSION

Understanding how species traits interact with changes in environmental conditions to mediate community alteration can help
FIGURE 3 Streamflow anomalies measured as extreme (a) high and (b) low flow ($\gamma_{hf}$, $\gamma_{lf}$) intensities, and (c) signal-to-noise ratio from 1948 to 2012 throughout the Upper and Lower Colorado River. SNR reflects the relation between predictable (seasonal) flows relative to stochastic flows. Blue triangles denote location of major dams and date of completion of each dam. Discharge was measured as liters per second from USGS data [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 Streamflow anomalies measured as extreme (a) high and (b) low flow ($\gamma_{hf}$, $\gamma_{lf}$) intensities, and (c) signal-to-noise ratio from 1948 to 2012 throughout the Alabama-Coosa-Tallapoosa River and Apalachicola-Chattahoochee-Flint basins. SNR reflects the relation between predictable (seasonal) flows relative to stochastic flows. Blue triangles denote location of major dams and date of completion of each dam. Discharge was measured as liters per second from USGS data [Colour figure can be viewed at wileyonlinelibrary.com]
FIGURE 5 Species richness of native freshwater fishes within individual sub-basins (U.S. Geological Survey [USGS] Hydrologic Unit Code 8 [HUC8]) of the (a) Upper and Lower Colorado River (CR), and (b) Alabama-Coosa-Tallapoosa and Apalachicola Chattahoochee-Flint River basins. Numeric values within HUC8s refer to the number of species extirpated from historical to present-day (see Materials and methods for details) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Binomial logistic regression models selected for all-possible subsets of covariates (n = 14), treated as fixed effects, on extirpation probability of native freshwater fishes within individual sub-basins (U.S. Geological Survey [USGS] Hydrologic Unit Code 8 [HUC8]) Upper and Lower Colorado River (CR), Alabama-Coosa-Tallapoosa (ACT), and Apalachicola-Chattahoochee-Flint (ACF) basins. Model covariates included: species traits (flow dependent, length and age at maturity, aspect ratio, longevity, fecundity, egg size), streamflow anomalies (extreme low and high flows, signal-to-noise ratio [SNR]), sub-basin characteristics [distance (km) upriver, km impounded, dam isolated], and sub-basin nonnative species richness. SNR reflects the relation between predictable (seasonal) flows relative to stochastic flows. Percentage (%) difference in odds is calculated as the (odds ratio /C0 /C1) 9 100, where the odds ratio is the exponent of the regression coefficient (estimate). Quantitative covariates were centered using z-scores. Binary covariates were not centered. Model selection was determined using the bestglm package in R

| Basin | Model covariates | Estimate | SE  | z value | Pr(|z|) | Odds ratio | % Difference |
|-------|------------------|----------|-----|---------|--------|------------|--------------|
| ACF   | Intercept        | −6.55    | 0.67| −9.71   | 2.61E-22 | 607.89     | 6E04          |
|       | Age at maturity  | 6.41     | 0.92| 6.99    | 2.85E-12 | 8.02E-05   | 28.50         |
|       | Dam isolated     | 3.35     | 0.85| 3.94    | 8.54E-05 | 2.34       | 134           |
|       | Fecundity        | 2.26     | 0.33| 6.74    | 1.54E-11 | 9.58       | 858           |
|       | Distance (km) from mouth | 0.85 | 0.23 | 3.74 | 1.80E-04 | 2.01       | 101           |
|       | Longevity        | −6.82    | 0.97| −7.03   | 2.04E-12 | 0.001      | −100          |
| ACT   | Intercept        | −252.83  | 707.64| −0.36 | 7.21E-01 | 9.9E05     | 9.9E07        |
|       | Flow dependent   | 16.11    | 705.18| 0.02  | 9.82E-01 | 9.9E05     | 9.9E07        |
|       | Length at maturity| 9.25 | 1.90 | 4.78 | 1.11E-06 | 1E04       | 1E06          |
|       | Age at maturity  | 3.98     | 1.23| 3.23    | 1.24E-03 | 53.52      | 5.252         |
|       | Distance (km) from mouth | 0.70 | 0.19 | 3.71 | 2.07E-04 | 2.01       | 101           |
|       | Egg size         | −0.60    | 0.23| −2.56   | 1.04E-02 | 0.55       | −45           |
|       | Longevity        | −15.84   | 2.70| −5.86   | 4.54E-09 | 0          | −100          |
|       | Fecundity        | −909.02  | 232.47| −3.91 | 9.22E-05 | 9.22E-05   | 9.22E-05     |
| CR    | Intercept        | −0.88    | 0.09| −9.88   | 5.20E-23 | 5.20E-23   | 5.20E-23     |
|       | Longevity        | 0.50     | 0.10| 4.78    | 1.76E-06 | 1.65       | 65            |
|       | Egg size         | −0.28    | 0.10| −2.68   | 7.33E-03 | 0.76       | −24           |
|       | Flow seasonality | −0.45    | 0.09| −5.01   | 5.51E-07 | 0.64       | −36           |
quantifying current and impending extirpation risk (Moore & Olden, 2017; Zavala et al., 2009). Trait-based approaches in stream ecology allow for a mechanistic understanding of species distribution and abundance by considering environmental constraints or “filters” imposed across the range of hierarchical spatio-temporal scales (Chessman, 2013; Poff, 1997; Rolls & Stemberg, 2015). Thus, they may allow for a better understanding of the relationships between environmental change and threats to native species persistence. For example, increases in stream temperatures select for smaller body size among fishes (Daufresne, Lengfellner, & Sommer, 2009), and both small- and large-bodied species can have high extinction risk in ecosystems with degraded habitat (Olden, Hogan, & Vander Zanden, 2007). In addition, determining species sensitivity vs. adaptation to changing environmental conditions needs to be considered in the context of evolutionary life history. Although we found more extreme streamflow events in selected basins in the Southwest than in the Southeast, such findings may simply reflect differences in the natural flow regime between these regions rather than extreme flows that could generate ecological disturbances (sensu Poff, 1992).

Species traits interact with environmental changes to mediate community disassembly among contrasting hydroclimatic regions undergoing strong hydrologic alterations (both climate and human-modified). We found that effects of dams and climate change on decreasing streamflow variance and anomalies were greater in Southwest than Southeast rivers. We measured higher magnitude changes in streamflow anomalies, a distinct shift in the seasonality of discharge, and stronger effects of dams on reducing discharge variance in the Southwest than the Southeast (Figures 3 and 4). However, presence of dams disproportionately affected extirpation risk of species isolated in upland streams of the ACF and of flow-dependent species in the ACT (Table 1). Extirpations have been relatively evenly distributed across sub-basins in the Southwest (Figure 5a). By contrast, extirpation risk in the Southeast was greater in upland basins than in lowland basins of the Upper ACT and ACF, where dams impede migratory species and restrict the ranges of endemic headwater fishes (Figure 5b). Despite higher magnitudes in hydrologic alteration in the Southwest, the density and distribution of dams in Southeast rivers, especially in the ACT (Figure 4a–c), increase extirpation probabilities even in these diverse fish assemblages (Figure 5b). In both regions (Southwest and Southeast), species life histories and geographic ranges, and hydrologic alterations explained extirpation probabilities. Our findings are critical, as we need to understand impending extinctions among river basins worldwide that have many threatened native species (Arthington, Dulvy, Gladstone, & Winfield, 2016; Jelks et al., 2008; Vörösmarty et al., 2010). Further understanding of how extirpation risk among native fish species may vary among regions with different levels of biodiversity (e.g., Weeks et al., 2016) is needed to enhance global species conservation.

Variation in streamflow is a critical driver of native species persistence even in highly invaded regions (Rolls et al., 2012; Ruhı, Holmes, Rinne, & Sabo, 2015; Ruhı et al., 2016). Our multi-basin analysis of historical vs. present-day occurrences indicates that extreme low- and high-flow events as well as direct effects of dams on seasonal variability in streamflow, likely contribute to localized fish extinctions. A recent analysis of native and nonnative species abundances from multiple Southwest rivers found that quasi-extinction risk, defined as the probability of 80% decline within 10 years, is higher for native than non-native fishes and is intensified by low-flow anomalous discharge (Ruhı et al., 2016). Trends of declining discharge throughout the Southwest suggest that native species will continue to be negatively impacted by projected increases in drought, whereas non-native fishes are predicted to replace collapsed native fish communities (Ruhı et al., 2016). Water withdrawals and reduced streamflows will continue to threaten the persistence of southwestern fishes into the future (Gido et al., 2010; Jaeger et al., 2014).

Climate-driven changes in discharge may continue to be stronger drivers of species vulnerability in Southwest than Southeast rivers. Although many freshwater fishes listed as imperiled are from Southeast rivers (Jelks et al., 2008), populations of these listed species have remained persistently static, implicating range restriction effects from upland dams as opposed to continual declines in habitat (Freeman et al., 2005). Overall decreases in—and shifts in the timing of—precipitation, as well as increases in mean temperatures, are forecasted for the American Southwest (Seager et al., 2013). In the American Southeast, on the other hand, most climate models indicate increases in precipitation, with simultaneous evaporation increases resulting in reduced runoff (Seager, Tzanova, & Nakamura, 2009). Droughts are typically shorter in duration with greater variability in occurrence in the Southeast than in the Southwest, which increases projection uncertainty for drought frequency and severity in the Southeast compared to the Southwest (Seager et al., 2009). Both regions have experienced unprecedented population growth, and the potential for changing energy demands linked to water pose one of the greatest water resources challenges moving forward (McDonald et al., 2012).

Recent decades have witnessed heightened attention on advancing the science underpinning environmental flow management for river conservation (Arthington, 2012; Poff et al., 2010). Achieving ecological integrity of flowing waters, including flow and temperature requirements of many native freshwater species, is a tremendous challenge; yet, evidence from across the world demonstrates its potential to conserve native fishes (Olden et al., 2014). The use of hydroclimatic models to understand past hydrological changes is a critical first step, followed by predictive models that forecast when and where alterations are likely to occur and compromise ecological integrity. Modeling efforts need to quantify environmental uncertainty across multiple temporal and spatial scales to dynamically adjust conservation priorities. Understanding where extirpation probabilities are high and can be attributed to specific abiotic and biotic variables plays an important role in setting conservation priorities. Furthermore, understanding where uncertainties in both predictor and estimator variables are high may guide monitoring and restoration efforts (Wenger et al., 2013).
It is clear that natural flow variability and sufficient water availability are essential to maintaining ecological health and native species persistence in streams and rivers (Ruh et al., 2015, 2016; Sabo et al., 2010). To advance effectiveness of restoring regulated flow regimes, we must move beyond the study of isolated extreme flow events to integrated time series of hydroclimatic changes and their effects on native and nonnative communities and ecosystem functions (Gillespie, Desmet, Kay, Tillotson, & Brown, 2014; Olden et al., 2014). Protecting environmental needs for flow variability and water security need to be prioritized through adaptive management approaches that include (i) regional environmental flow targets (Poff et al., 2009), (ii) setting human water-use ceilings that are sufficiently constrained to meet environmental needs across variable (high and low) flow conditions (Bunn & Arthington, 2002), and (iii) holistic hydropower planning that uses models and technologies to minimize biological impairment (McDonald et al., 2012; Winemiller et al., 2016). The former strategy is often prescribed in basins that have imperiled species present but is rarely implemented. Furthermore, increases in human water-use efficiency (reduction in consumptive use) are rarely made to allow for meeting environmental needs, rather those efficiencies are made for expanding human water use (Richter, 2010).

 Adequate environmental flows in a river basin indicate that all water allocations and dam regulations are being managed in a sustainable manner, such that the net outcome of human and environmental water needs is attained (Richter, 2010). To enhance ecological integrity, flow regimes need to be designed to meet specific ecological outcomes that more effectively inform water management decisions using existing infrastructure (Acreman et al., 2014; Poff et al., 2016). We must shift prioritization from restoring reference conditions (e.g., natural flow regime) or discrete large-scale flow experiments (Olden et al., 2014) to prescribe flows that increase native species resilience and help mitigate extirpations with forecasted climate-driven changes in streamflow. Dams will continue to represent barriers for species dispersal, but if seasonal flow patterns and large-scale flow releases are designed to enhance hydromorphologic and ecological connectivity, novel flow regimes could achieve sustainable ecological outcomes.

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