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Application of a New Species-Richness Based Flow Ecology Framework for Assessing Flow Reduction Effects on Aquatic Communities

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Research Impact Statement: Quantification of change in fish species richness from streamflow reductions provides a regional water-resources risk assessment management tool.

ABSTRACT: Water-resources managers are challenged with maintaining a balance among beneficial uses throughout river networks and need robust means of assessing potential risks to aquatic life resulting from flow alterations. This study generated ecological limit functions from species-streamflow relations to quantify potential fish richness response to flow alteration and compared results to currently accepted streamflow management guidelines. Modeled responses of absolute richness change were watershed specific and varied among sample sets derived from hydrologic unit classifications of different sizes (large HUC 6 basins to regional scale HUC 8). With a 20% flow reduction, 10% of HUC 8 predicted a richness decrease in one or more taxa. While absolute richness change was consistent across streams within a HUC, percent richness change was stream size dependent. Comparisons with Instream Flow Incremental Methodology habitat models predicted habitat loss greater than percent richness change; however, predictions for habitat and richness decreased similarly as stream size decreased. Watershed-specific responses from flow reductions could allow water-resources management decisions to be made locally based on the predicted richness change for certain sized streams. Quantitative results highlight the utility of a richness-based framework for generating watershed-specific risk assessments that validate and inform currently employed water-resources management practices.

(KEYWORDS: richness; ecological limit function (ELF); water-resources management; fish; habitat; withdrawal; elfgen.)

INTRODUCTION

Water-resources managers are responsible for overseeing a wide range of beneficial uses throughout the river network, with multiple uses for public use, industry, agriculture, energy, assimilative capacity, recreation, navigation, and to support aquatic biota. The flow needs of aquatic biota often play a crucial role in determining water available for withdrawal; however, generalized rules for estimating ecological responses to flow alteration have been difficult to determine (Poff and Zimmerman 2010). Due to understanding gained through years of adaptive management, application of the Instream Flow Incremental Methodology (IFIM), and ecological flow principles, and the simplicity of implementation, many streams in Virginia are now managed with an allowable

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"percent-of-daily-flow diversion" schema. These schemas are characterized by daily varying withdrawal limits and reservoir releases that mimic the natural hydrograph (Richter et al. 2012), by ensuring that only a percent-of-daily-flow is diverted, often in the range 10%–20% of the previous day's mean flow. Percent-of-daily-flow diversions are widely believed to be protective by practitioners, particularly when flow alteration is below 10%. While these management schemas succeed in mimicking the natural range of high and low flows, they result in a net reduction in flows, and cost-effective methods of quantifying the impacts to fish species richness from these net reductions of flow were lacking.

IFIM studies have been a preferred method of flow management, because they provide objective means of quantifying risk to aquatic species by developing extensive habitat maps and then modeling the decrease to habitat that occurs when flows are reduced. In this way, habitat loss becomes an estimate of ecological risk. However, without direct experimentation or long-term population monitoring it can be difficult to directly quantify the species richness or abundance responses associated with given amounts of habitat loss. One alternative, the Ecological Limits of Hydrologic Alteration (ELOHA) method (Poff et al. 2010), advocates for constructing daily timestep hydrologic models with withdrawals, discharges and impoundments to estimate pre- and post-alteration flow metrics. The "space-for-time" approach requires paired biological samples with modeled streamflow. This approach was used to estimate ecological responses to flow alteration in Virginia (Rapp and Reilly 2017), but representative, suitable paired biological and hydrological locations were not abundant, and habitat change was not quantified. ELOHA has the potential to be less expensive and time consuming than IFIM models, but suffers from limitations in flow-model accuracy, lack of prealteration flow data, and low data density. The IFIM and ELOHA experimentation in Virginia led us to seek an alternative approach to quantifying the impacts to fish species richness from flow reductions.

The approach in this study applied the River Continuum Concept (RCC) hypothesis (Vannote et al. 1980) to instream flow management. The RCC postulates the predictive strength of drainage area (DA), streamflow, or stream order in determining richness or density in aquatic communities (Schlosser 1987; Beecher et al. 1988; Angermeier and Schlosser 1989; Walters et al. 2003; Filipe et al. 2010; Pracheil et al. 2013; Vander Vorste et al. 2017). Numerous studies are consistent with the RCC, that streams with higher streamflow volume have the potential to support richer fish assemblages, and have found that fish and benthic macroinvertebrates show negative responses to flow reductions (Freeman and Marcinek 2006; Dewson et al. 2007; Döll and Zhang 2010; Poff and Zimmerman 2010; Armstrong et al. 2011; Rolls et al. 2012; Gido et al. 2013; McManamay et al. 2013; Carlisle et al. 2014; Kennen et al. 2014; Knight et al. 2014; Brooks and Haeusler 2016; Rapp and Reilly 2017; Vander Vorste et al. 2017). Instead of examining the suite of typical ecological flow statistics like base flow index or seven-day low flow, we sought to examine potential fish response to a net reduction in mean annual flow (MAF). Recent studies have also used mean monthly flow (MMF) alteration by applying hydrologic models (Eng et al. 2013; Carlisle et al. 2014).

We applied "elfgen" methods developed with Kleiner et al. (2020) to generate ecological limit functions (ELF) that describe relations between flow and species richness predicted by the RCC. The RCC ELF framework, employing Virginia's extensive fish monitoring database, provides an alternative method for assessing flow depletion impacts without the need for extensive habitat characterization or in-depth flow modeling. The automated methods for batch generation of ELFs (Kleiner et al. 2020) use an approach that is simple to conceptualize and implement, to relate the entire Virginia long-term fish dataset (1970–2012) to nationally available MAF or MMF streamflow datasets from the medium scale (1:100,000) National Hydrography Dataset Plus Version 2 (NHDPlus V2) Enhanced Runoff Method (EROM) and catchments (U.S. Geological Survey and U. S. Environmental Protection Agency 2012). Given the increased pressure on freshwater resources in the Mid-Atlantic and the common practice of various percent-of-daily-flow diversions (Richter et al. 2012; Commonwealth of Virginia 2015; Hain et al. 2018; John Kauffman, Virginia Department of Game and Inland Fish, written Commun., October 19, 2004), the ELFs developed should be timely and useful tools in quantifying changes in richness from flow reductions at a range of watershed scales. In this paper, we examined variation in ELFs developed for Virginia's watersheds and explored the extent to which ELF equations might provide a practical means for prediction and quantification of ecological response to water-resources management activities, which should be applicable to other states in the mid-Atlantic. We characterized regional patterns of ELF slope and quantified the sensitivity of richness and habitat to flow reduction to inform water-resources management.

The objectives this study addressed were to: (1) Examine fish richness patterns discerned from ELFs developed with "elfgen" automated methods (Kleiner et al. 2020) at varying spatial scales. (2) Use the ELF slope to calculate rate of change in richness across varying spatial scales and annual or monthly flows. (3) Compare ELF richness change predictions to IFIM habitat change predictions. (4) Explore the extent to which ELFs can be used as an estimate of risk of richness change to inform water-resources management.

Study Area

The ELFs were developed for streams throughout Virginia and adjacent rivers that flow into Tennessee, West Virginia, North Carolina, Kentucky, or Maryland. The landscape is diverse in topography with ecoregions ranging from the South Eastern Coastal Plains with low-gradient, high-base flow blackwater streams; to Piedmont streams with moderate gradients, predominantly agricultural land use, and complex hard rock geology; to Blue Ridge, Ridge and Valley, or Appalachian Plateaus with steep topography, shallow soils, and high runoff regimes (Nelms et al. 1997). The study area, composed of 8 six-digit hydrologic unit classifications (HUC 6), and 51 eight-digit HUC 8 watersheds (U.S. Geological Survey 2014), contains first-order to seventh-order streams (Figure 1). The average precipitation ranges from 35 to 71 in per year and the majority of streams are perennial. MAF in rivers calculated from NHDPlus EROM datasets range from 0.004 to 15,989 ft^3/s (U.S. Geological Survey and U. S. Environmental Protection Agency 2012). The EROM datasets are calibrated to United States Geological Survey (USGS) gages and represent long-term (1971–2010) flow regimes for each stream.

METHODS

Two explore patterns of maximum species richness across Virginia we constructed RCC ELF models that utilize the 80th quantile or "upper limit" of species richness as a function of stream size represented by MAF or MMF. A few key concepts from Kleiner et al. (2020) are presented here to explain our use of the "elfgen" package for the creation of the ELF and facilitate interpretation of our results. Fish species richness (total number of taxa) from sample data in the Virginia long-term biological dataset (Tetra Tech Inc 2012; Kleiner et al. 2020) was plotted against the MAF using a combination of quantile regression and linear regression to examine patterns of species richness related to the RCC. DA is known to be correlated with MAF in Virginia which ranges from 0.42 to 0.76 ft^3/s per square mile depending on the region of the state (Nelms et al. 1997). The NHDPlus V2 attributes of MAF and DA for biological sample locations within each HUC 6 were found to be highly correlated (0.97–0.99, $p < 0.0001$, Figure S1). Since the focus on this work was to develop ELFs that inform water withdrawal decisions, MAF was used as the independent variable in these relations, but was highly correlated with DA within a given watershed.

Quantile regression was used to isolate the maximum richness values across a MAF gradient. The piecewise Iterative Method (PWIT) in Kleiner et al. (2020) implements breakpoints (Lemoine 2012) to subset the data to include only those samples that follow the pattern of greater species richness with larger MAF (i.e., at the inflection point between positive and negative relations of richness and MAF). The 80th quantile was used to isolate the upper 20% of the data (upper subset) and provided enough data to run a natural log-linear regression through the upper subset to characterize the mean condition of samples with the maximum species richness (Figure 2). The slope of the natural log-linear regression (Equation 1) represents the rate of change in richness as a function of changes in flow (Kleiner et al. 2020).

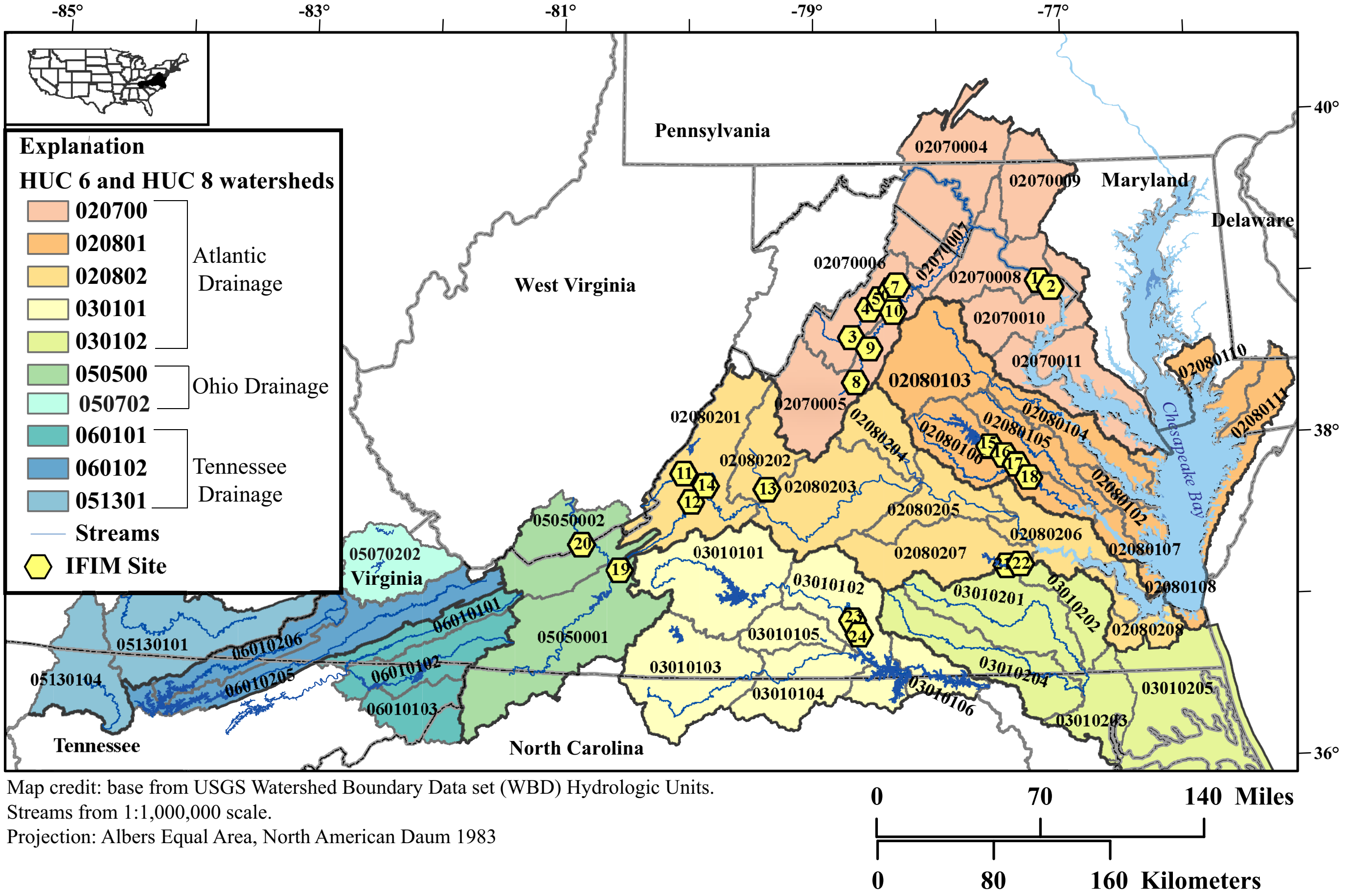
The ELF model is described by the following equation:

$$y = m \times \ln(x) + b, \tag{1}$$

where m and b are, respectively, the slope and intercept of the ELF of the upper subset, x refers to the MAF, and y is the maximum richness value for a biological sample location. Regression statistics derived from the ELF equation include R^2, adjusted-R^2, p-value, and number of data points, n which are presented at the bottom of each ELF plot (Figure 2). ELF were developed first for all HUC 6 and then for all HUC 8 watersheds in the study area.

Practical Implications for Building ELFs at Different Scales

In practice, to develop ELF to describe the upper limit of species richness and calculate rate of richness change, biological samples were extracted from a dataset to represent a geographic area or local watershed conditions. As we worked with various scales and sizes of watersheds the most consistent results were constructed with at least 80–100 samples in the full dataset so that the upper subset contained at least 16–20 records. HUC 6 watersheds ranged from 66 to 309 samples in the upper subsets, whereas HUC 8 watersheds ranged from 4 to 122 samples in the upper subsets and were generally within these guidelines. The smaller the watershed or geographic area used to extract data the more longitudinal



Map credit: base from USGS Watershed Boundary Data set (WBD) Hydrologic Units.
Streams from 1:1,000,000 scale.
Projection: Albers Equal Area, North American Daum 1983

FIGURE 1. Virginia six-digit hydrologic unit classifications (HUC 6) and HUC 8 watersheds with Instream Flow Incremental Methodology (IFIM) study site locations (IFIM site numbers relate to site information in Table S1. Site information and habitat information from published studies: Leonard et al. (1986); Maryland Department of Natural Resources (1981); Averett et al. (2004); Krstolic et al. (2006); Gore (2006); Thomas R. Payne and Associates (2008); EA Engineering Science and Technology Inc (2009); Krstolic and Ramey (2012).

discontinuities in stream conditions (Poole 2002) may be minimized. Biological samples within streams from a small, local watershed would be tightly linked to the local flow regime and similar habitat conditions and are likely to produce quality ELF models when adequate data are available.

Exploring Richness Patterns Using Breakpoints

The RCC breakpoint (Figure 2) represents a shift in the slope of the ELF upper subset of maximum richness values from increasing to decreasing or to a flat, zero slope. RCC breakpoints were developed for all watersheds across the commonwealth of Virginia to identify the threshold or inflection point beyond which species richness decreases as MAF increases, and therefore to indicate the size of rivers for which the RCC is applicable and valid. Breakpoints were determined using the PWIT function on biological sample data extracted from eight HUC 6 watersheds. HUC 6 breakpoints were then applied to 51 HUC 8 watersheds contained therein to provide insight into processes driving regional patterns of species richness and habitat heterogeneity across Virginia.

Spatial Distribution of ELF Slopes

We examined ELF slope and regression model summary statistic variability across two watershed unit scales (HUC 6, HUC 8), and level III ecoregions (U.S. Environmental Protection Agency 2013). The distribution of slopes and R^2 values from each that were significant and met quality criteria such that $R^2 > 0$, $p \leq 0.01$, and slope $(m) > 0$ were included. The interquartile range of R^2 and slope values was compared to assess the effect of watershed unit size from which the biological data were compiled and used to construct ELFs.

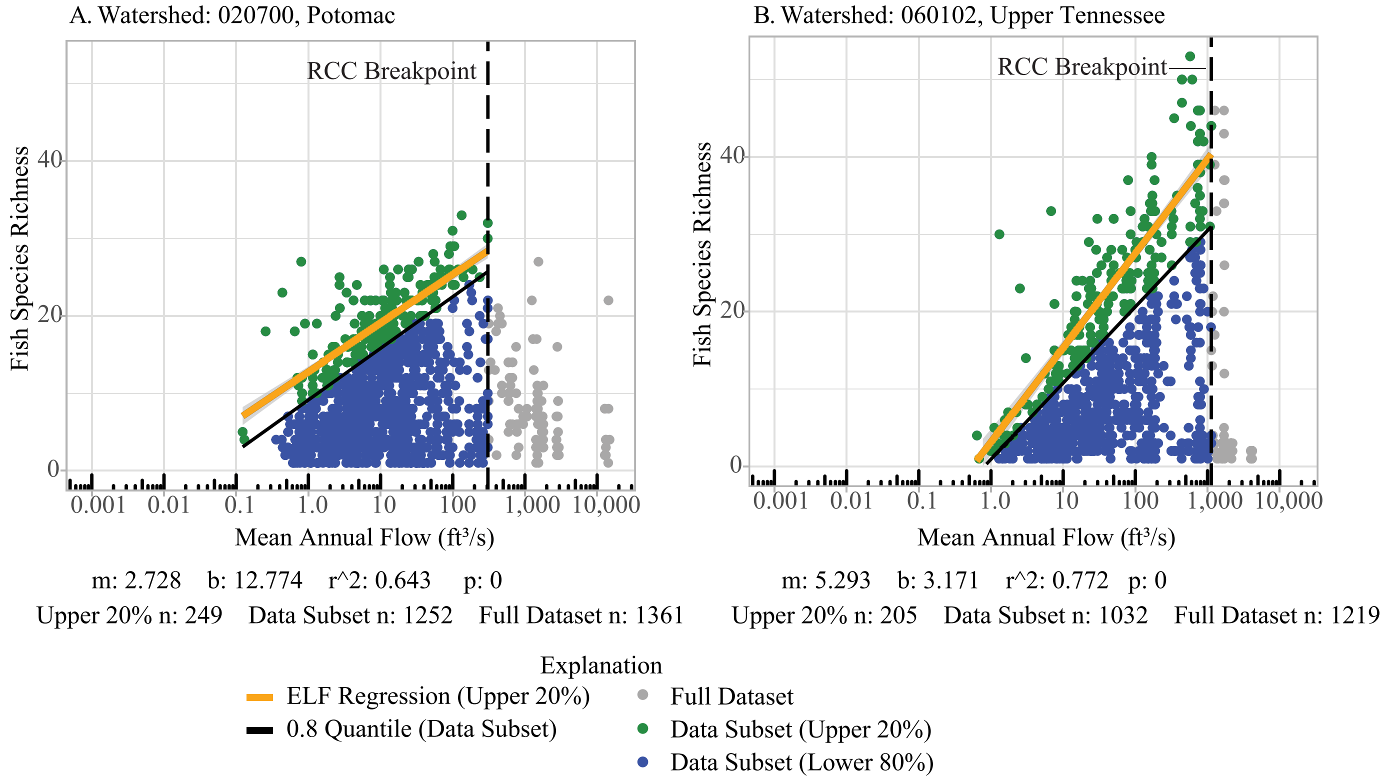


FIGURE 2. Ecological limit function (ELF) plots of fish total taxa richness and mean annual flow (MAF) for (a) Potomac HUC 6 and (b) Upper Tennessee HUC 6. [ELF Equation 1 elements are presented below the figure (m, b, r^2 and p-value). Considering the Potomac HUC 6, data subset (green points, n = 249) represents the extracted biological sample locations greater than the 80th percentile which were used as input to the ELF regressions. Data subset (blue points, n = 1,252) represents biological sample locations below the 80th quantile. The full dataset (n = 1,361) includes the grey points that are associated with MAF greater than the breakpoint. To create an ELF all biological samples from streams of all sizes are extracted from the geographical extent of each HUC 6 (see the inset map). See Kleiner et al. (2020) for more details about ELF generation. RCC, River Continuum Concept.]

Calculating Rate of Change in Richness. The initial patterns of maximum species richness that were observed along the MAF gradient in the RCC ELFs supported our hypothesis that these linear relations were robust representations of the rate of increase in richness along the MAF gradient. An assumption which could then be applied is that richness would decrease along the MAF gradient following the same constant rate if water were removed from the system. This assumption allows the derivation of the rate of richness change as a function of flow. The natural log-linear regression model (Equation 1) for the upper subset for each significant HUC 6 or HUC 8 ELF was solved to characterize absolute richness change for 10 and 20% flow reduction scenarios using Equation (2).

$$\text{Change in Species Richness} = \Delta y = m \times \left[\ln\left(\frac{1}{1-z}\right)\right], \tag{2}$$

where Δy is the change in richness (number of taxa or species), m is the slope of the ELF, and z is the percent reduction in flow (as a decimal). Richness change as a constant number resulted in one numeric rate for any size stream within a given ELF, but these numbers varied across HUCs.

The ELF models also were used to calculate the percent change in species richness for a range of MAF represented by increments of 0.1 ft^3/s from 0.1 to 500 ft^3/s using Equation (3).

$$\text{Percent Change in Species Richness} = \frac{\Delta y}{y_1} = \frac{m \times \left[\ln\left(\frac{1}{1-z}\right)\right]}{m \times \ln(x_1) + b} \times 100, \tag{3}$$

where Δy is the change in richness, y_1 is the initial richness value, m is the slope of the ELF, z is the percent reduction in flow (as a decimal), and x is the initial flow value. The percent change in species richness developed using Equation (3) was incremental along the MAF gradient depending upon the total richness present in the stream of interest prior to flow reductions.

Percent Change in Habitat, a Case Study of IFIM Data

We compiled and processed habitat information for 24 IFIM sites throughout Virginia to assess habitat change associated with monthly flow reductions. At IFIM sites (Figure 1; Table S1) analyses were conducted to validate the ELF approach with previously published habitat models that report habitat area for a given streamflow (Maryland Department of Natural Resources 1981; Leonard et al. 1986; Averett et al. 2004; Krstolic et al. 2006; Gore 2006; Thomas R. Payne and Associates 2008; EA Engineering, Science, and Technology Inc 2009, 2012; Krstolic and Ramey 2012). Percent change in habitat was calculated using MAF, MMF, and 10th percentile flows for 24 IFIM sites ranging from 192 to 5,000 mi^2 encompassing streams within the range represented by the RCC ELFs and larger. The published IFIM tables of Weighted Usable Area (WUA for a specified streamflow were applied to the historic daily flow record and used to calculate percent change in habitat for each month and each fish species using Equation (4).

$$\text{Percent change in habitat} = \sum \text{month}\left[\frac{\text{Daily WUA historic} - \text{Daily WUA 10\% reduction}}{\text{Daily WUA historic}} \times 100\right], \tag{4}$$

where Daily WUA historic is the daily WUA habitat value for a given species based on the historic flow record, Daily WUA 10% reduction is the daily WUA habitat value for a given species based on a 10% flow reduction applied to each day of the historic record. The percent change in habitat daily values were summarized for annual and monthly time periods for each individual species or the community median response to flow reductions following similar techniques demonstrated in Hoffman (2015).

Where valid ELF and IFIM sites coincided percent change in habitat predictions were compared with the corresponding ELF percent change in species richness values. Percent change in species richness from ELFs and median percent change in habitat from WUA predictions were developed for August monthly flow reductions for the HUC 8 that contained the IFIM habitat site to represent seasonal conditions when habitat degradation is usually greatest (Averett et al. 2004; Krstolic et al. 2006). We developed ratios of *percent change in species richness: percent change in habitat* to examine whether the habitat and species richness increased or decreased at the same or a constant predictable rate for various flow reduction scenarios.

RESULTS AND DISCUSSION

RCC Breakpoints Indicate Richness Thresholds

Use of the PWIT (Kleiner et al. 2020) resulted in identification of RCC breakpoints for all eight HUC 6 analyzed (Table 1). The HUC 6 within the Atlantic and Ohio River drainages had RCC breakpoints representing stream sizes with MAF ranging from 307 to 408 ft^3/s (8.7–11.6 m^3/s). HUC 6 in the Tennessee River drainage had the highest breakpoints, representing streams with MAF ranging from 1,122 to 1,126 ft^3/s (31.8–31.9 m^3/s) (Table 1; Figure S2). Across the study area, 93.5% of streams had MAF less than their RCC breakpoint and represent 124,575 river miles for which these ELFs can be used to examine effects of flow reductions on fish species richness.

The RCC breakpoints identified a maximum richness threshold that coincided with mid-order (fifth or sixth order) streams. In streams with MAF higher than the RCC breakpoint relative richness was less than in streams with MAF lower than the RCC breakpoint. This RCC breakpoint threshold may indicate the point at which local habitat complexity and heterogeneity begin to decrease. For example, the smallest streams in the Potomac River watershed had five to eight taxa, increasing up to 32 taxa at the RCC breakpoint of 307 ft^3/s (Figure 2). When MAF exceeded the RCC breakpoint richness was typically <20 taxa, and richness incrementally decreased as MAF increased up to 5,000 ft^3/s (Figure 2). These patterns of incrementally decreasing richness as streamflow increased for samples larger than the RCC breakpoint were typical for most of the Atlantic and Ohio River drainages, but were less prominent in the Albemarle-Chowan (030102) HUC 6 in far eastern Virginia and North Carolina (Figure 1) and the upper Tennessee HUC 6 (Figures 1 and 2; Figure S2).

Spatial Distribution of ELF Slopes

ELFs slopes varied depending upon whether sample sets were derived from HUC 6 large major river basins or smaller HUC 8 regional scale watersheds and based on ecoregion. Sufficient fish sample size (more than 100 in the full dataset) was available for the development of statistically significant ELFs for fish species richness for all eight HUC 6 watersheds, 33 of 51 HUC 8 watersheds, and seven ecoregions. ELFs with a wide range of slopes in HUC 8 watersheds are dispersed throughout different major basins (Figure 3a). HUC 6 slopes ranged from 1.6 to 5.4 (Table S2). The HUC 8 slopes generally followed

TABLE 1. RCC breakpoints for fish datasets derived from piecewise iterative method for ELF generation.

HUC or region name	HUC6	*N* samples	RCC breakpoint MAF, in ft^3/s	Drainage
Potomac	020700	1,363	307	Atlantic
Lower Chesapeake	020801	1,628	348	
James	020802	1,894	389	
Roanoke	030101	1,244	385	
Albemarle-Chowan	030102	712	408	
Kanawha (New)	050500	410	348	Ohio
French Broad-Holston	060101	1,317	1,122	Tennessee
Upper Tennessee	060102	1,222	1,126	

ecoregion boundaries with higher ELF slopes in areas that coincide with the Blue Ridge or Ridge and Valley ecoregions. The lowest ELF slopes occurred in the Southeastern Plains and Middle Atlantic Coastal ecoregions which have the lowest physical stream gradients of any region within the study area. When ELFs were developed for ecoregions, an east to west pattern of low to high slopes was observed (range = 0.0–3.5, Figure 3b), but the range of slopes for HUC 8 was much higher (range = 1.2–6.5 Figure 3a). There appears to an Ecoregion signature affecting these patterns, but the higher slopes in the HUC 8 were related to the maximum richness in each major drainage basin, also noted as an important variable by Angermeier and Winston (1999) and Hain et al. (2018). Quartile R^2 values were slightly lower for ecoregions than HUC 6 or HUC 8 (Table S2). Slopes for smaller watersheds had a somewhat greater diversity of rates of change than ecoregions (Table S2).

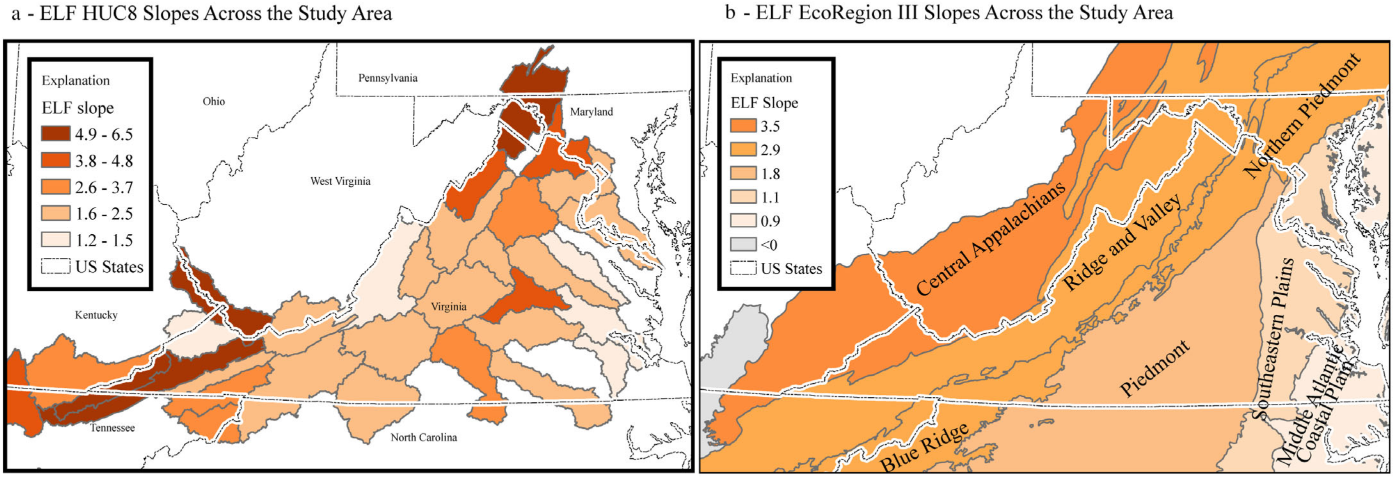
Average Richness Change. Richness change rates were constant across all size streams for a given ELF, and directly related to ELF slopes (Equation 2), so larger slopes resulted in greater potential richness change. With a 10% flow reduction, 90% of HUC 8 ELFs had richness change predictions of −0.5 taxa or less (Table 2), and none had richness change predictions as high as −1.0 taxa (Figure 4; Table 2). With a 20% flow reduction, 50% of HUC 8 ELFs had richness change predictions of −0.5 taxa or less. Ten percent of HUC 8 ELFs had richness change predictions as high as −1.0 taxa (Figure 4; Table 2). ELFs created for HUCs in the Upper Tennessee (060101, 060102) and Potomac River watershed (020700) had the highest slopes and the highest richness change predictions of all HUC 8 watersheds. For all HUC 6 and HUC 8 watersheds, the 10% flow-reduction scenarios had richness change predictions less than −1.0 taxa (Figure 4).

Richness Change as a Percent (%). While absolute richness change is a constant across all size streams for a given ELF, the percent change in species richness varies with flow volume (MAF) (Figure 5b). This is because small streams typically have lower richness and thus greater proportional changes in richness compared to larger streams within the same HUC 8. For example, when Equation (3) was solved for streams in the Middle-Potomac-Catoctin ELF (Figure 5) a 20% flow reduction resulted in −6.5% change in species richness for streams with MAF equal to 1 ft^3/s, but only −3.0% change for streams with MAF equal to 100 ft^3/s (Figure 5b). These richness change predictions are some of the highest across the study area because the slope of 3.8 is in the 75th percentile of slopes (Table 2). Across all HUC 8s in the study area, 20% flow reductions for streams equal to 10, 100, or 500 ft^3/s had median percent change in species richness values of −3.0%, −2.3%, and −1.9%, respectively (Figure S3).

Percent Habitat Change from IFIM Sites

A typical IFIM site (Laurel Hill, DA = 508 mi^2, MAF = 592 ft^3/s, Figure 1; Table 3) with a modeled 10% flow reduction resulted in seasonal increases in habitat during Spring and Winter months and decreases in habitat during Fall and Summer months (Figure S4). Percent habitat change for all species studied was negative (indicating habitat loss) in August, September, and October (Figure S4). Across all IFIM sites, August and September flows had the greatest rates of habitat loss with flow reduction, further supporting the use of August flows as an indicator of risk of habitat loss or richness change (Krstolic et al. 2006; Armstrong et al. 2011; Kennen et al. 2012; Krstolic and Ramey 2012; Knight et al. 2014; Commonwealth of Virginia 2015; McManamay and Frimpong 2015; Rapp and Reilly 2017). With a 20% flow reduction, most of the IFIM sites with MAF <900 ft^3/s had a median habitat-loss condition in August, and the majority of IFIM sites with MAF >900 ft^3/s had a median habitat-gain (Figure 6). Regardless of stream size, outliers at the bottom of each box indicated that habitat for some species always decreased with flow reduction (Figure 6).

With August MMF conditions, IFIM sites larger than the RCC breakpoint had stable or increasing


a - ELF HUC8 Slopes Across the Study Area

b - ELF EcoRegion III Slopes Across the Study Area

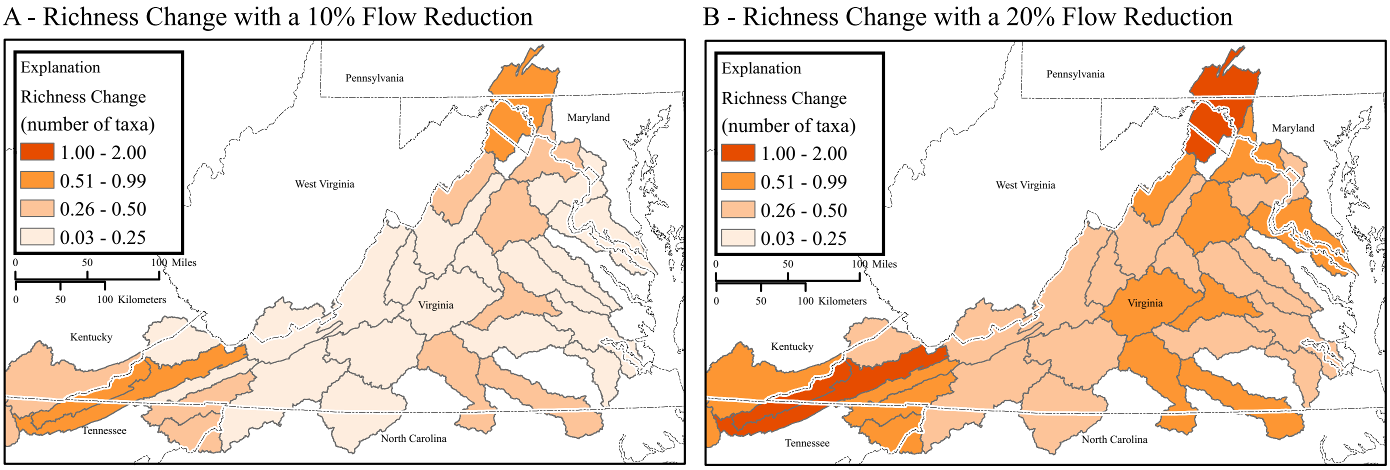
FIGURE 3. ELF slopes across (a) HUC 8 and (b) Level III Ecoregions (slope values in b represent the exact values for each ecoregion).

TABLE 2. Cumulative frequency distribution quantiles of HUC 8 slope and richness change predictions for 10% and 20% flow reductions. [Percent exceedance quantiles relate the number of ELFs that are equal to or below the category.]

Slope	Quantiles		10% Flow reduction richness change (number of taxa)	20% Flow reduction richness change (number of taxa)
6.5	100%	Maximum	−0.7	−1.4
4.9	90%		−0.5	−1.0
3.7	75%	Quartile	−0.4	−0.8
2.3	50%	Median	−0.2	−0.5
2.0	25%	Quartile	−0.2	−0.4
1.3	10%		−0.1	−0.3
1.2	0%	Minimum	−0.1	−0.3

median percent change in habitat with 20% flow reductions (Figure 6a); however, all 24 IFIM sites had habitat loss when flows were below the 10th percentile flow in summer months (Figure 6b). It follows that during extreme low flow as habitat is reduced species richness may also be reduced, corroborating the findings of Rapp and Reilly (2017) that many species responses were highly correlated with alterations of summer-month low-flow statistics.

Percent Change in Habitat and Richness at IFIM Sites. IFIM-based habitat change modeling has been widely used as a surrogate for aquatic organism response for the past 60 years; however, the use of the ELF predictions for richness change at the same locations with IFIM habitat models is a


A - Richness Change with a 10% Flow Reduction

B - Richness Change with a 20% Flow Reduction

FIGURE 4. Distribution of richness change values for each HUC 8 for two flow-reduction scenarios: 10% flow reduction (a); 20% flow reduction (b).

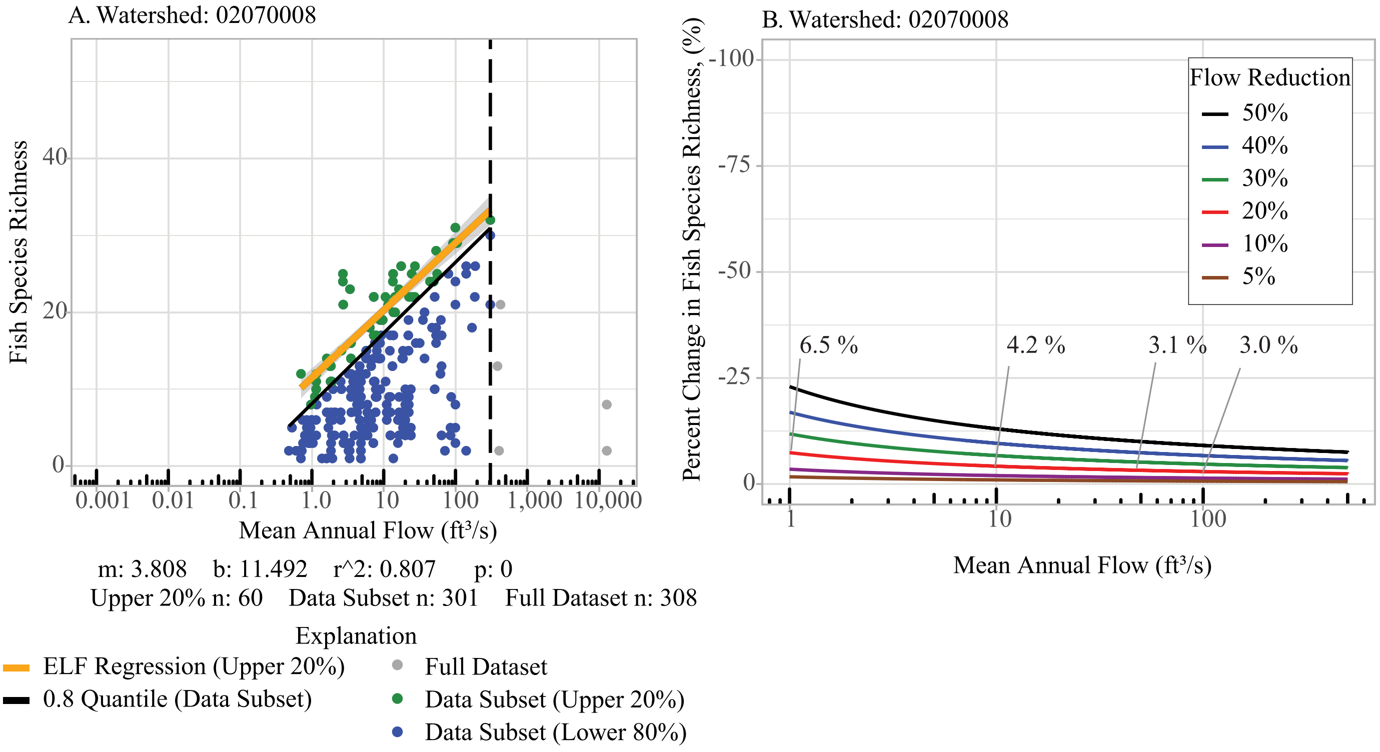


FIGURE 5. ELF plot for one HUC 8 watershed (a) and percent change in species richness plot for the same HUC 8 (b). (Part b labels highlight the predicted percent decrease in richness for a 20% flow reduction. For streams of size 1, 10, 50 and 100 ft^3/s the percent decrease in richness ranges from −6.5% to −3.0%. For locations see Figure 1.)

new effort toward quantitative assessment that has not been done before. For the HUC 8 watersheds that contain the IFIM sites ELF predictions of August percent change in species richness ranged from −0.6% to −1.3% and −1.2% to −2.7% for 10% and 20% flow reductions, respectively (Table 3; Figure S5). Predictions of median August percent change in habitat ranged from −0.9% to −6.2% and −1.8% to −12.2% for 10% and 20% flow reductions, respectively (Table 3). August percent change in species richness was less than the percent change in habitat for the IFIM sites (Figure 7). The five smallest IFIM sites (MAF range from 193 to 410 ft^3/s) were relatively close in area to their respective HUC 6 RCC breakpoints, so the flow reductions produced relatively low percent change in species richness.

Correlations between Percent Change in Richness and Percent Change in Habitat. Across IFIM sites, ratios of *percent change in species richness: percent change in habitat* for August ranged from 0.1 to 0.6 with a median of 0.2 for HUC 8 ELFs (Table 3) indicating that percent change in habitat was two times greater than percent change in species richness. Regardless of 10% or 20% flow reductions, the summer-month ratios were fairly stable because percent change in habitat and species richness increased in magnitude at constant rates with greater flow reductions. Like other habitat studies (Krstolic et al. 2006; Krstolic and Ramey 2012), we found that smaller streams had greater sensitivity to flow alteration resulting in percent change in habitat or richness. The August *percent change in species richness: percent change in habitat* models had a positive correlation, but were not statistically significant (corr = 0.3327, $p = 0.5194$; Table 3). This weak correlation is not unexpected given the small number of paired sites, and the fact that IFIM habitat relations are site-specific, representing 100s to 1,000s of feet of stream reach, whereas ELF relations cover the entire contributing area of a HUC. Nonetheless, ELF models though developed separately from the IFIM habitat studies, provided an initial quantification of richness change for each flow reduction scenario. The five IFIM site (Figure 7) sizes were within 10% of the RCC breakpoint for each containing HUC 8 and represent moderate size streams (order 4–5). IFIM models representing smaller sites (1–300 ft^3/s) would better approximate the risk within the range of stream sizes represented by the ELFs. In order to flesh out a more comprehensive and quantitative understanding of *percent change in species richness: percent change in habitat ratios*, long-term studies of

TABLE 3. Ratios of percent change in species richness and percent change in habitat for IFIM sites and 10% and 20% August flow reduction scenarios.

IFIM site name	Monthly flow (ft^3/s)	Flow reduction scenario (%)	Habitat Median percent change in habitat (%)	Richness: Percent change in species richness from HUC8 ELF	Richness: HUC8 ratio %change in species richness: % change in habitat	Richness: HUC8
Craig	410.8	10	−0.95	−0.6	0.6	2080201
Dunlap	193.3	10	−5.23	−0.6	0.1	2080201
North Anna Coastal Plain	392.3	10	−6.21	−0.8	0.1	2080106
North Anna Fall Zone	400.8	10	−5.23	−0.8	0.2	2080106
North Anna Piedmont	375.0	10	−1.56	−0.8	0.5	2080106
Plains Mill	315.0	10	−4.96	−1.3	0.3	2070006
Craig	410.8	20	−1.84	−1.2	0.6	2080201
Dunlap	193.3	20	−11.08	−1.2	0.1	2080201
North Anna Coastal Plain	392.3	20	−12.68	−1.7	0.1	2080106
North Anna Fall Zone	400.8	20	−12.21	−1.7	0.1	2080106
North Anna Piedmont	375.0	20	−3.26	−1.7	0.5	2080106
Plains Mill	315.0	20	−10.41	−2.7	0.3	2070006

both could be conducted at the same locations along a stream size gradient.

Limitations of Habitat and ELF Models

Seasonal patterns of percent change in habitat were opposite from percent change in species richness during high-flow months, but both decreased during low-flow months (July through October). Differences in model predictions resulted from differing model forms and fisheries datasets. Both models represent flow using a log-scale, but IFIM WUA curves relate available habitat area for each species to daily streamflow that were summarized to monthly median habitat change for multiple species, whereas ELFs relate total species richness to MAF or monthly flows. The link between the ELF and IFIM results depends on the species sampled at the IFIM site being representative of those sampled in streams throughout the HUC 8. The natural log-linear ELF is a representation of relative change based on one rate (slope) for the entire HUC calculated from long-term mean flows, whereas the WUA curves represented habitat available at time-varying flow value, that may present a limiting condition under extreme or short-term time scales that differ from the median values calculated in this study. More sophisticated hydrologic models with higher spatial and temporal resolution could potentially produce ELFs based on flow metrics that are comparable to WUA, but the linear ELF simple model is easily interpretable, has high explanatory power, and applicability anywhere there are NHDPlus river reaches.

CONCLUSIONS

In examining fish richness patterns depicted by 33 significant ELFs for HUC 8 watersheds we found the upper subset of species richness data corroborated the RCC as species richness was positively correlated with MAF up to a threshold or breakpoint beyond which the species richness decreased as MAF continued to increase. The ELF slope was a key variable that indicated the magnitude of rate-of-change in richness expected for a watershed. Slopes tended to be higher when the ELF represented a more diverse assemblage which is important to note since it suggests that not all watersheds will respond to flow reductions the same way. In watersheds with very diverse assemblages smaller streams have the capacity to support higher richness, but with higher ELF slopes, the projected rate of change is also high, so

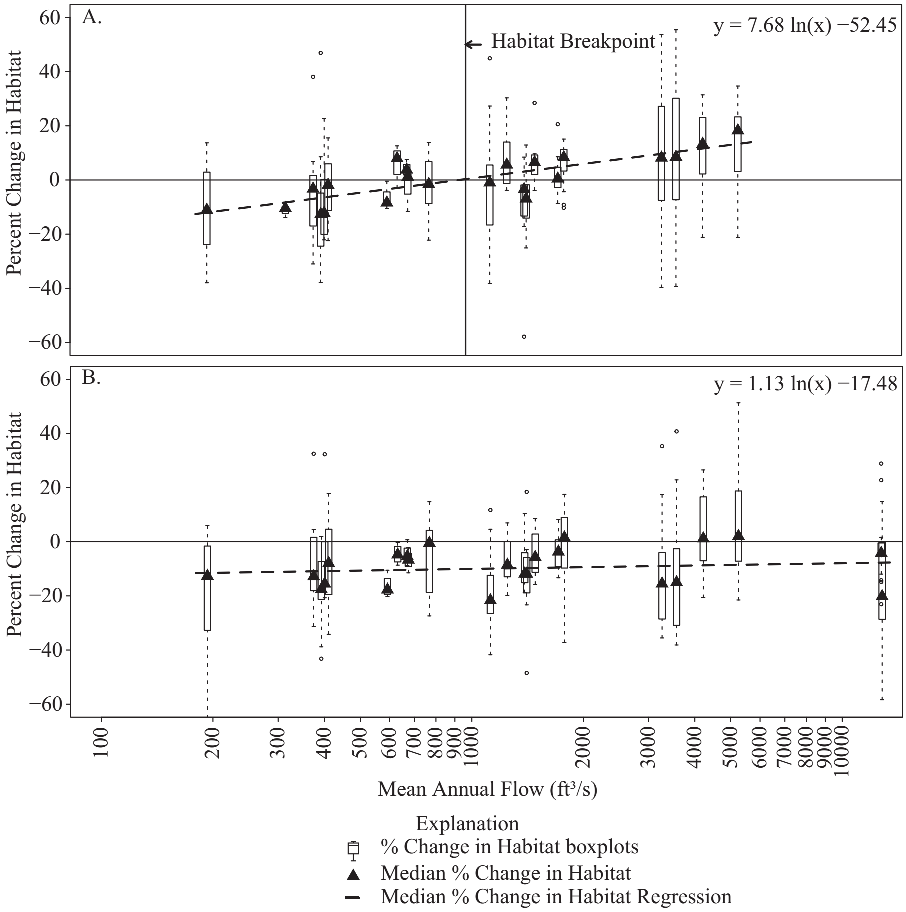


FIGURE 6. August Median percent change in habitat for each IFIM site plotted by MAF for (a) 20% flow reduction, and (b) 20% flow reduction during flows lower than the 10th percentile of the historic period of record, representing extreme low flow (Each box represents percent change in habitat for multiple species studied at the IFIM site. Each box represents the August box from a site like the one represented in Figure S4. The dashed line is a regression of the median percent change in habitat. 10th percentile flow plots include additional sites that contained pertinent data for the Potomac River. For IFIM site information see Table S1).

the risk to richness loss is greater than it would be in watersheds that have lower species richness.

The coupling of ELF richness-change predictions with IFIM habitat-change predictions represent a first attempt to link and quantify habitat and richness change in Virginia. The general patterns of change during low-flow months were similar, but predictions of percent habitat change were typically two times greater than predictions of richness change. ELF simulations of flow reductions in large streams (MAF = 193–410 ft^3/s) produced relatively low percent change in species richness. Smaller streams had greater sensitivity to percent change in habitat or richness with flow alteration. Additional habitat and ELF evaluations of small streams would help to flesh out the relations in future analyses. Our examination of habitat response to depletion of 10th percentile flows also suggests that MAF-based ELF studies might not adequately represent crucial effects of water reductions during low flows. Future studies using ELFs based on drought flow metrics should be explored, and streams that are larger than the RCC breakpoint examined to further evaluate the utility of the ELF framework. While we do not suggest that ELF analyses can replace IFIM habitat studies entirely, ELFs can be used to predict the risk of species richness loss with flow reductions for each size stream within a watershed. They could be used to identify areas requiring additional aquatic community sampling, widespread streamflow monitoring, or more detailed analysis of watersheds predicted to have high percent change in species richness), at a fraction of the cost of an IFIM study.

The predictions of richness change derived from ELFs can be used to assess the potential harm or risk to aquatic communities from flow reductions. The findings from the predicted richness change evaluations from 10% and 20% flow reductions were consistent with percent-of-daily-flow best practices recommended by agency biologists in use today

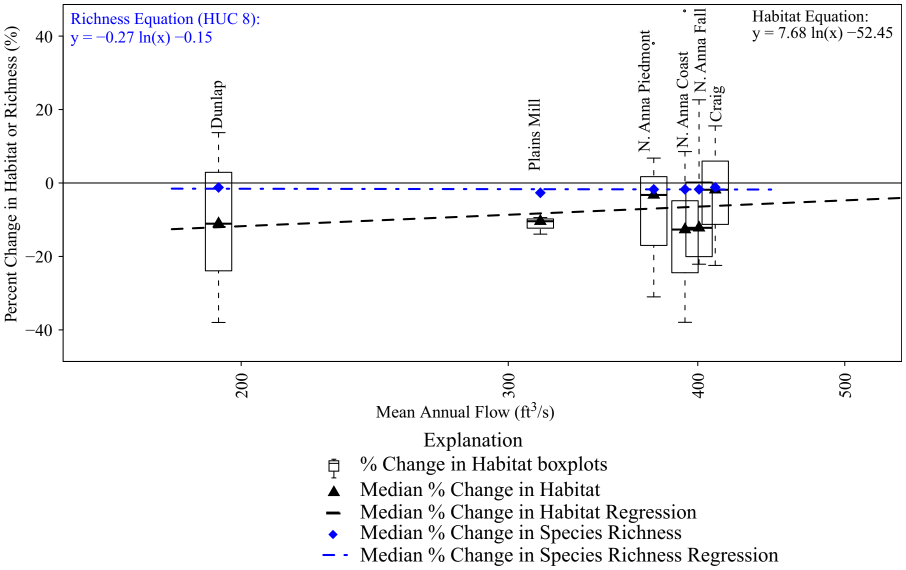


FIGURE 7. August predictions for percent change in habitat and percent change in species richness with a 20% flow reduction at IFIM sites with MAF <530 ft^3/s [Dunlap and Craig Creeks are in the Upper James River watershed (02080201), Plains Mill is in the North Fork Shenandoah River watershed (02070006), and the North Anna sites are in the Pamunkey River watershed (02080106)].

(Richter et al. 2012; Rosenfeld 2017; Hain et al. 2018). As an initial tool to prioritize water withdrawal permits at regional scales, ELF richness change predictions and existing percent allocation information could be used to determine withdrawal amounts which could be potentially protective of species richness.

SUPPORTING INFORMATION

Additional supporting information may be found online under the Supporting Information tab for this article: Five supplemental figures illustrating the relation between mean annual flow across HUC 6, ELFs for fish species richness in HUC 6 watersheds throughout the Commonwealth of Virginia, percent richness change results for a range of stream sizes, IFIM monthly percent habitat change predictions for one typical site, and select ELFs representing August flow in HUC 8 watersheds that contain IFIM sites. Two supplemental tables describing the IFIM published model site locations referenced in this study, and the distributions of R^2 and slopes of ELFs are presented as Supporting Information.

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AUTHORS' CONTRIBUTIONS

Jennifer L. Rapp: Conceptualization; formal analysis; investigation; methodology; project administration; writing-review & editing. **Robert Burgholzer:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; validation; writing-review & editing. **Joseph**

Kleiner: Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing-review & editing. **Durelle Scott:** Conceptualization; investigation; methodology; validation; writing-review & editing. **Elaina Passero:** Conceptualization; data curation; software; visualization.

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