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RELATIONS BETWEEN ALTERED STREAMFLOW VARIABILITY AND FISH ASSEMBLAGES IN EASTERN USA STREAMS[†]

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ABSTRACT

Although altered streamflow has been implicated as a major factor affecting fish assemblages, understanding the extent of streamflow alteration has required quantifying attributes of the natural flow regime. We used predictive models to quantify deviation from expected natural streamflow variability for streams in the eastern USA. Sites with >25% change in mean daily streamflow variability compared with what would be expected in a minimally disturbed environment were defined as having altered streamflow variability, based on the 10th and 90th percentiles of the distribution of streamflow variability at 1279 hydrological reference sites. We also used predictive models to assess fish assemblage condition and native species loss based on the proportion of expected native fish species that were observed. Of the 97 sites, 49 (50.5%) were classified as altered with reduced streamflow variability, whereas no sites had increased streamflow variability. Reduced streamflow variability was related to a 35% loss in native fish species, on average, and a >50% loss of species with a preference for riffle habitats. Conditional probability analysis indicated that the probability of fish assemblage impairment increased as the severity of altered streamflow variability increased. Reservoir storage capacity and wastewater discharges were important predictors of reduced streamflow variability as revealed by random forest analysis. Management and conservation of streams will require careful consideration of natural streamflow variation and potential factors contributing to altered streamflow within the entire watershed to limit the loss of critical stream habitats and fish species uniquely adapted to live in those habitats. Published in 2011 by John Wiley & Sons, Ltd.

KEY WORDS: natural flow regime; predictive models; hydrologic modification; fish assemblages

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INTRODUCTION

The patterns of floods, droughts and variability in streamflow shape the instream habitats that influence the aquatic biota in a stream (Bunn and Arthington, 2002). Studies have shown that streams with low streamflow variability have fish assemblages that are very different in structure and function than streams that experience high streamflow variability (Poff and Allan, 1995). A study of New England streams (Bain *et al.*, 1988) reported that highly variable streamflow may affect fish differently depending on how they use stream habitat. However, Meador and Matthews (1992) suggested that high streamflow variability does not necessarily represent a disturbed environment to fish assemblages if such variability is part of the natural flow regime. Although studies have examined relations between streamflow variability and fish assemblages (e.g. Horwitz, 1978; Bain *et al.*, 1988; Poff and Ward, 1989; Meador and Matthews, 1992; Poff and Allan, 1995; Herbert and Gelwick, 2003), most have been based on observed variations in streamflow that could be attributed to natural or anthropogenic sources, or both. Thus, quantifying the variability inherent in the natural flow regime is necessary to better understand the ecological effects of anthropogenic alterations of streamflow variability (Poff and Zimmerman, 2010).

Although the natural flow regime must be quantified to assess hydrological alteration, doing so has been a difficult challenge (Arthington *et al.*, 2006). Poff and Zimmerman (2010), in a review of 165 studies of aquatic responses to modified streamflow, indicated that a variety of approaches have been used to characterize attributes of the natural flow regime (in addition to the biological response). Such characterizations are often based on historic (e.g. pre-disturbance) flow records (Richter *et al.*, 1996, 1997; Henriksen *et al.*, 2006; Poff *et al.*, 2007) or modelled using data from nearby stream gauges. However, pre-disturbance flow records are limited for most gauged streams and non-existent for ungauged streams. Carlisle *et al.* (2010) developed empirical predictive models that quantified site-specific expected characteristics of the natural flow regime in gauged and ungauged rivers and streams. These models produced nationally consistent, accurate estimates of natural streamflow variability measured as the annual coefficient of variation (CV) of daily streamflow. By determining the deviation of observed streamflow variability from estimates

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of natural streamflow variability, Carlisle *et al.* (2010) were able to quantify alteration of streamflow variability and demonstrate that altered streamflow variability was sensitive to water management and land use (Carlisle *et al.*, 2010).

Data collected as part of the U.S. Geological Survey's (USGS) National Water-Quality Assessment (NAWQA) Program provided the opportunity to study relations between fish assemblages and altered streamflow variability. Our specific objectives were as follows: (i) to evaluate relations between altered streamflow variability and native fish species richness; (ii) to evaluate the relative importance of fish species ecological traits in predicting altered streamflow variability; (iii) to evaluate relations between the severity of altered streamflow variability and the likelihood of fish assemblage impairment; (iv) to assess relations between altered streamflow variability and potential physicochemical covariates; and (v) to evaluate the relative importance of selected hydrology related environmental factors in predicting altered streamflow variability.

METHODS

Study area

The NAWQA Program's design focuses on major river basins across the USA (Gilliom *et al.*, 1995). Major river basins were selected based on several factors including population and water use, importance of water-quality issues and geographic distribution. River basin selection focused on agricultural and urbanized basins and used forested basins to reflect undisturbed land use. Whereas the river basins are geographically distributed across the USA, their locations are biased towards areas where population and water use are greater than average. Additional information on the NAWQA Program can be found at http://water.usgs.gov/nawqa/.

This study was limited to the eastern half of the USA because predictive models of expected native fish species composition have been developed for streams in the eastern USA (Meador and Carlisle, 2009) but have not been developed for western streams because of low native species richness (Meador *et al.*, 2008). These predictive models allow for regionally consistent estimates of native fish species loss in eastern USA streams. In order to assess changes in native fish species richness relative to altered streamflow variability, we selected 28 river basins within the eastern USA, defined here as east of the 100th meridian, or 100°W longitude (Figure 1).

Streamflow variability

We defined streamflow variability as the annual CV (standard deviation/mean) of daily streamflow values. The CV is a relatively simple expression of the magnitude of discharge variability (Horwitz, 1978) and has been reported to be an important measure of average streamflow conditions (Olden and Poff, 2003). We averaged the annual CV over a period of at least 20 years of streamflow records. Twenty years has been reported to be the minimum period of record for obtaining reliable estimates of streamflow characteristics (Richter *et al.*, 1997; Huh *et al.*, 2005; Henriksen *et al.*, 2006).

We assessed whether streamflow variability was altered at each gauged site by applying the models of Carlisle *et al.* (2010) to estimate an expected average annual CV under reference conditions, based on statistical models developed with 1272 hydrological reference sites located across the USA and streamflow records from 1980 to 2007. The absolute quality of reference sites varied across the USA. For example, in the Midwest, with long histories of intense landscape alteration, reference sites were 'least disturbed' or in 'best available' condition (*sensu* Stoddard *et al.*, 2006). Carlisle *et al.* (2010) reported that national models based on site-specific natural watershed attributes outperformed any regionally stratified models, and thus we used the national models developed by Carlisle *et al.* (2010). Model validation at reference sites showed that estimates of daily CV were unbiased (mean observed/expected = 0.99) and relatively precise (standard deviation of observed/expected = 0.24) (Carlisle *et al.*, 2010). For additional information on reference sites and model development, see Carlisle *et al.* (2010).

We quantified the alteration of streamflow variability based on the ratio of the observed mean annual CV (O_{cv}) to the expected reference value from the model (E_{cv}). We then classified each site as altered if O_{cv}/E_{cv} exceeded the 10th or 90th percentile of the distribution of O_{cv}/E_{cv} across the 1272 references sites used to construct the model. This approach is similar to that used in assessing biological condition (Hawkins, 2006). Sites with O_{cv}/E_{cv} ratios less than the 10th percentile of reference site values ($O_{cv}/E_{cv} < 0.75$) were classified as having reduced streamflow variability relative to expected and would therefore have streamflow variability that was statistically less than would be expected in a minimally disturbed environment. Sites with O_{cv}/E_{cv} ratios greater than the 90th percentile of hydrological reference site values ($O_{cv}/E_{cv} > 1.25$) were classified as having increased streamflow variability relative to expected and would therefore have streamflow variability that was statistically greater than would be expected in a minimally disturbed environment. All remaining sites were classified as unaltered, having streamflow variabilities that were statistically similar to expected natural streamflow variability. In addition to classifying sites based on streamflow variability condition, we used O_{cv}/E_{cv} values as a measure of the per cent change in streamflow variability at a site, calculated as $(O_{cv}/E_{cv} - 1) * 100$.

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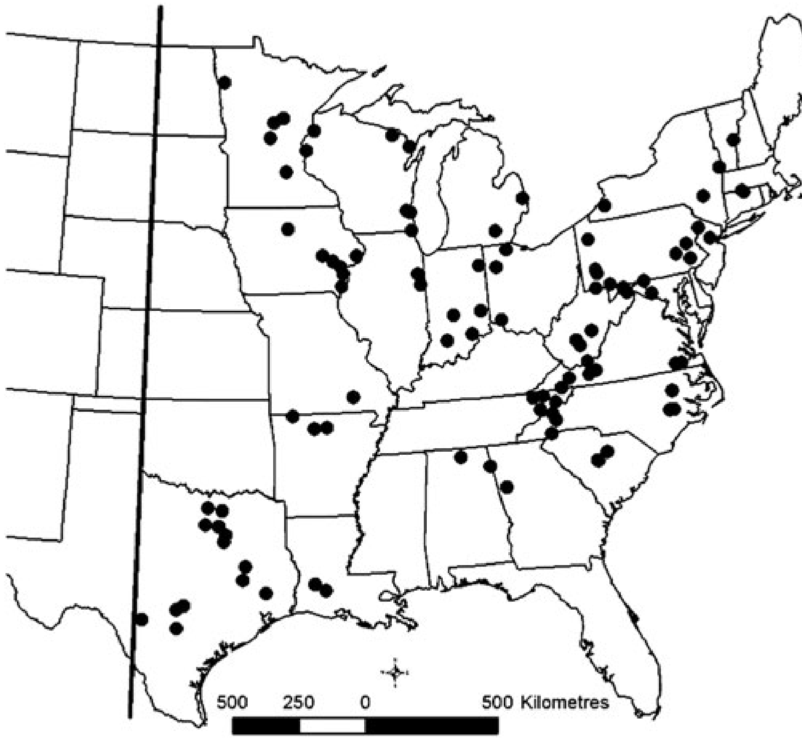

Figure 1. Location of 97 sites in the eastern USA assessed for streamflow variability and fish assemblage condition. Line represents 100th meridian.

Fish sampling

A sampling reach was identified at each site with reach lengths determined based on the presence of a variety of habitat types (pools, riffles and runs) and meander wavelength. Attempts were made to include at least two examples each of two different habitat types. When this was not possible, reach length was determined based on a distance of 20 times the mean channel width, roughly equivalent to one meander wavelength (Fitzpatrick *et al.*, 1998). A minimum reach length of 150 m and a maximum reach length of 300 m were established prior to sampling for wadeable sites. Minimum and maximum reach lengths for non-wadeable sites were 300 and 1000 m, respectively.

Fish were collected during low flow using a standard sampling protocol based on a combination of two-pass electrofishing and seining (Moulton *et al.*, 2002). Operators of electrofishing gear received training in the sampling protocol and in electrofishing principles, such as power transfer theory in order to help standardize electrofishing efforts and increase the efficiency of electrofishing operations (Reynolds, 1996). Fish were identified to species and counted. Fish that could not be identified in the field were retained for identification in the laboratory. Taxonomic identifications in the field and laboratory were made or supervised by trained ichthyologists (Walsh and Meador, 1998).

Assessing fish assemblage condition

Fish assemblage condition was assessed using models to predict taxonomic completeness, defined as the difference between the observed and expected native species composition (Meador and Carlisle, 2009). Taxonomic completeness was quantified based on the proportion of expected native fish species that were observed (*O*/*E*). Meador and Carlisle (2009) developed models for the eastern USA (east of the 100th meridian) based on 266 biological reference sites. Independent regional and local criteria were used to identify biological reference sites based on factors including watershed and riparian land use, reach-scale physical and chemical characteristics and consultation with local biologists. Similar to hydrological reference sites, the absolute quality of biological reference sites also varied. For example, biological reference sites in the New England states were selected primarily based on watershed land cover (<5% urban and <20% row-crop agriculture) and therefore approximate the definition of least disturbed or best available by Stoddard *et al.* (2006). In contrast, biological reference sites in the predominantly agricultural Midwest were largely selected by using best professional judgment of local biologists usually based on the degree of intact riparian zones. Such biological reference sites therefore approximate 'best attainable' (*sensu* Stoddard *et al.*, 2006) conditions.

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Meador and Carlisle (2009) developed regionally based models to account for the effects of natural zoogeographic patterns and environmental gradients. Meador and Carlisle (2009) reported that models of fish taxonomic completeness predicted fish species composition at reference sites with relatively high precision and low bias and provided model predictions of taxonomic completeness that were standardized and nationally consistent. Model predictions at test sites were sensitive to land use at the watershed scale and eastwide. For additional information on the fish predictive models, see Meador and Carlisle (2009).

Meador and Carlisle (2009) selected the 10th percentile of *O*/*E* values at biological reference sites ($O/E = 0.75$) as the threshold below which fish assemblages were classified as 'impaired', otherwise samples were classified as 'unimpaired'. The authors did not consider an upper threshold of impairment (90th percentile) because it is unclear whether assemblages with *O*/*E* values >1 are impaired (Hawkins, 2006). By using an *O*/*E* value of 0.75 as a criterion, Meador and Carlisle (2009) judged that a >25% loss of native species expected to occur was sufficient to classify a site as impaired. The per cent of expected native fish species that were absent was also assessed and used to estimate native species loss, calculated as $(1 - O/E) * 100$.

Fish ecological traits

For each site, we identified fish species with preferences for specific habitats (riffle, pool, run and backwater) and substrates (cobble, gravel, sand and vegetation) based on information by Goldstein and Meador (2004). We also identified all fish species as fluvial specialists or macrohabitat generalists based on information in Kinsolving and Bain (1993), Mettee *et al.* (1996) and Hartel *et al.* (2002). Fluvial specialists are species requiring flowing-water habitats throughout their lives. A fish species identified as a fluvial specialist may occasionally be found in a reservoir or lake but is typically associated with lotic habitats. Conversely, macrohabitat generalists can be found in both lotic and lentic environments. The models used to assess biological condition (Meador and Carlisle, 2009) were also used to predict trait-based taxonomic completeness, defined as the difference between the observed native species with a particular trait that were among the expected native species with that trait ($O_{\mathrm{Trait}}/E_{\mathrm{Trait}}$).

Potential covariates with altered streamflow variability

Selected potential covariates with altered streamflow variability included both physical habitat and physicochemical water-quality variables. Habitat variables that could potentially be related to altered streamflow included the ratio of pools to riffles, variation in water depth, the ratio of wetted channel width to water depth and the per cent frequency of occurrence of silt. Instream habitat data were collected following standard protocols based on a transect-point design (Fitzpatrick *et al.*, 1998). The per cent pools and riffles were determined based on the relative proportion of the total length of the sampling reach that was composed of pool or riffle habitats. The CV in water depth was determined based on the total number of sampling points of depth in metres. The frequency of occurrence of silt within a sampling reach was calculated by dividing the number of occurrences by the number of sampling points. For additional information on habitat data collection, see Fitzpatrick *et al.* (1998).

Physicochemical water-quality variables included total phosphorus ($\mathrm{mg\,L^{-1}}$), total nitrogen ($\mathrm{mg\,L^{-1}}$), specific conductance (μS at 25 °C) and water temperature (°C) and were sampled using standardized methods (Shelton, 1994). Several litres of water were composited from depth-integrated or width-integrated samples. From the composited sample, 250–1000 mL splits were extracted and preserved in the field for laboratory analyses of phosphorous and nitrogen concentrations. Data quality was maintained through adherence to quality assurance plans and quality-control samples (e.g. replicates, field blanks, spikes). Water temperature was measured directly from the stream using hand-held probes. Specific conductance was measured from split samples. Only chemistry data collected within 14 days of fish collections were included in this analysis.

Factors influencing stream hydrology

Geographic information systems (GIS) analysis was used to assemble basin-level hydrological and land-cover data. Stream networks were obtained from the USGS National Hydrography Dataset (USGS, 2004a). Watershed boundaries (USGS, 2004b) were digitized at the 1:24 000 scale to determine drainage basin areas. We calculated measures of factors thought to influence stream hydrology using available GIS databases including the density of constructed water conveyance systems in the basin (waterways identified as canals or ditches), reservoir storage, the distance to the nearest dam, the density of dams, the density of major permitted wastewater discharges, water withdrawals, the density of roads and the number of road–stream intersections within a basin (Table I). The density of dams was based on dams >2 m in height (USACE, 2006). Major permitted water discharges were designated by the U.S. Environmental Protection Agency (USEPA, 2006) and included wastewater discharges with design flows $>3.786 \times 10^6$ L (1×10^6 gal). Major wastewater discharges include municipal wastewater facilities, industrial discharges and point-source storm water runoff. The number of road–stream intersections was determined per kilometre of total basin stream length.

Table I. Variables and data sources for factors that influence stream hydrology

Variable	Units	Data source
Canals	% of waterways in watershed	Horizon Systems (2006)
Dams	number km^{-2}	USACE (2006)
Nearest dam	km	USACE (2006)
Permitted discharge	number km^{-2}	USEPA (2006)
Reservoir storage	L km^{-2}	USACE (2006)
Road density	km km^{-2}	GeoLytics (2001)
Road–stream intersections	number km^{-1} total stream length	GeoLytics (2001)
Water withdrawal	10^6 L km^{-2}	USGS (2000)

Data analysis

The non-parametric Kruskal–Wallis rank test was used to determine whether the per cent loss of expected native species varied among classes of altered streamflow variability. The Kruskal–Wallis test was also used to assess variation in the ratio O_{Trait}/E_{Trait} for each trait among classes of altered streamflow variability. In addition, the factors influencing stream hydrology were assessed among classes of altered streamflow variability. All differences were declared to be statistically significant when p was less than 0.05.

Conditional probability analysis (CPA; Paul and McDonald, 2005) was conducted to plot the probabilities of observing fish assemblages in impaired condition over a gradient of altered streamflow variability. For each unique value of the per cent change in streamflow variability, CPA calculates the proportion of observations with greater per cent changes in streamflow variability that are classified in impaired fish condition. A positive slope was taken as evidence that the severity of streamflow variability alteration, in the presence of all other factors, was associated with the likelihood of fish assemblage impairment. Spearman correlation analysis was conducted to assess relations between per cent change in streamflow variability and covariates.

We performed random forest classification analysis (Breiman, 2001; Cutler *et al.*, 2007) to predict classes of streamflow variability from fish ecological traits and from the factors influencing stream hydrology. The classification output from the random forest analysis represents the statistical mode of many classification decision trees, thereby achieving a more robust model than a single-classification tree produced by a single-model run (Breiman, 2001). Random forest analysis provides for the determination of variable importance measures and prevents problems associated with correlated variables and overfitting (Breiman, 2001).

We conducted random forest analysis by fitting 500 classification trees each with a bootstrapped sample of 70% of the observations where a randomly selected subset of the predictor variables was considered at each branch. The remaining 30% of observations were passed through each tree to evaluate predictive performance. On average, each observation was omitted from 1/3 of the trees, and the final prediction for each observation was obtained by averaging the predictions across all the trees where it was excluded. This cross-validation produces estimates of classification error that are close to what would be expected with independent data (Carlisle *et al.*, 2010).

The relative importance of predictors was evaluated using the Gini index, a measure of node impurity, or the degree to which a variable produces terminal nodes in the forest of classification trees (Breiman *et al.*, 2006). Splitting a node on a variable causes the Gini impurity for the two descendent nodes to be less than the parent node. The Gini index is the sum of the decreases in impurity for a variable across the forest of classification trees and provides a measure of variable importance by indicating how often a predictor variable was selected and its relative overall discriminatory ability.

RESULTS

A total of 97 sites were included in data analyses (Figure 1). Observed streamflow variability was 32–115% of the predicted reference values (mean $O_{cv}/E_{cv} = 0.76$ or 24% reduced streamflow variability). None of the sites were classified as altered because of increased streamflow variability (i.e. >125% of reference). Forty-nine sites (50.5%) had O_{cv}/E_{cv} values that were less than 0.75 and thus classified as altered with reduced streamflow variability. The remaining 48 sites were classified as an unaltered streamflow variability condition. At sites classified as having reduced streamflow variability, loss of expected native fish species (mean = 35.6%) was significantly higher ($p = 0.001$) than at sites classified as having unaltered streamflow variability (mean native species loss = 4.9%) (Figure 2).

The probability of an impaired fish assemblage increased with increasing severity of reduced streamflow variability (Figure 3). A greater than 0.50 probability of an impaired fish assemblage was associated with reductions in streamflow variability in excess of 9%. Relatively few observations were noted at reductions in streamflow variability greater than

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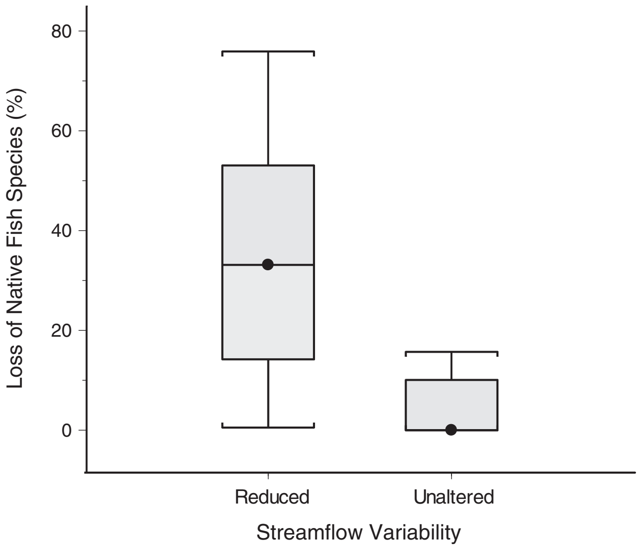

Figure 2. Plot of loss of expected native fish species richness for sites classified as having reduced ($N=49$) and unaltered ($N=48$) streamflow variability. Boxes show medians and quartiles, whiskers indicate 10th and 90th percentiles.

about 40%, resulting in relatively large confidence intervals (Figure 3). Spearman correlations between per cent reduced streamflow variability and covariates were greatest for total nitrogen (rho = 0.39) and total phosphorous (rho = 0.30). No other rho values were greater than 0.25.

Random forest analysis indicated that fish ecological traits predicted streamflow variability with an overall accuracy of 72.2% and correctly classified 79.2% of unaltered streamflow variability sites and 65.3% of sites with reduced streamflow variability. Species with preferences for riffle habitats had the highest Gini index (8.3) followed by fluvial-specialist species (7.9). Gini index values for all other traits ranged from 2.2 to 6.1 (Figure 4). Values of $O_{\mathrm{Trait}}/E_{\mathrm{Trait}}$ for all traits were significantly different between sites with reduced and unaltered streamflow variability (Table II). The median loss of species with preferences for riffle habitat and fluvial-specialist species was >59% at sites with reduced streamflow variability.

Random forest analysis indicated that factors that influence stream hydrology predicted streamflow variability with an overall accuracy of 77.3% and correctly classified 79.2% of unaltered streamflow variability sites and 75.5% of sites with reduced streamflow variability. Reservoir storage had the highest Gini index (10.1) followed by wastewater discharges (8.9) (Figure 5). Remaining variables had Gini index values ranging from 4.2 to 5.5. Kruskal–Wallis analyses indicated that reservoir storage, wastewater discharges, per cent canals and road density were all significantly greater, and the distance to the nearest dam was significantly less, at sites with reduced streamflow variability compared with sites with unaltered streamflow variability (Table III). No other factors that influence stream hydrology were significantly different between sites with reduced and unaltered streamflow variability.

DISCUSSION

This study quantifies for the first time the severity of altered streamflow variability and associated condition of fish

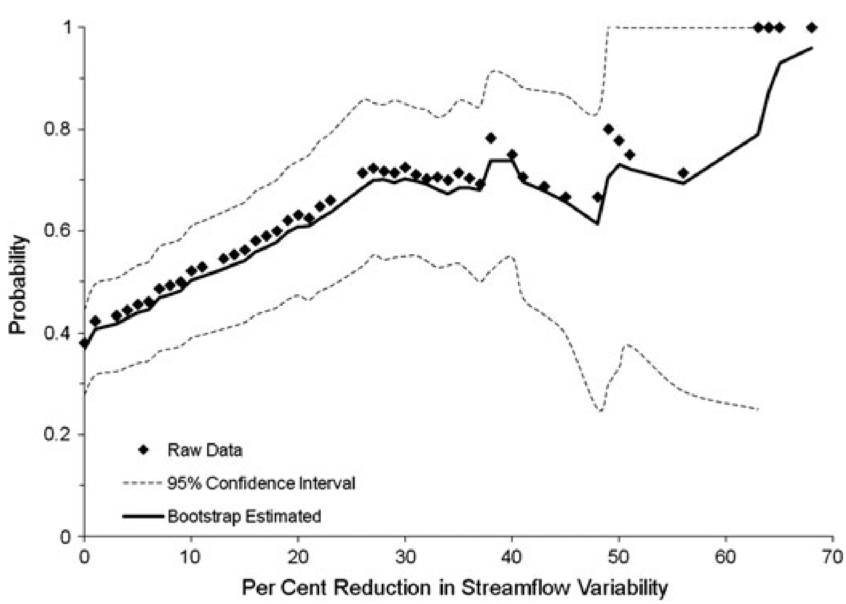

Figure 3. Probability of impaired fish assemblages with increasing severity of reduced streamflow variability. Smoothing and 95% confidence intervals were generated with bootstrapping.

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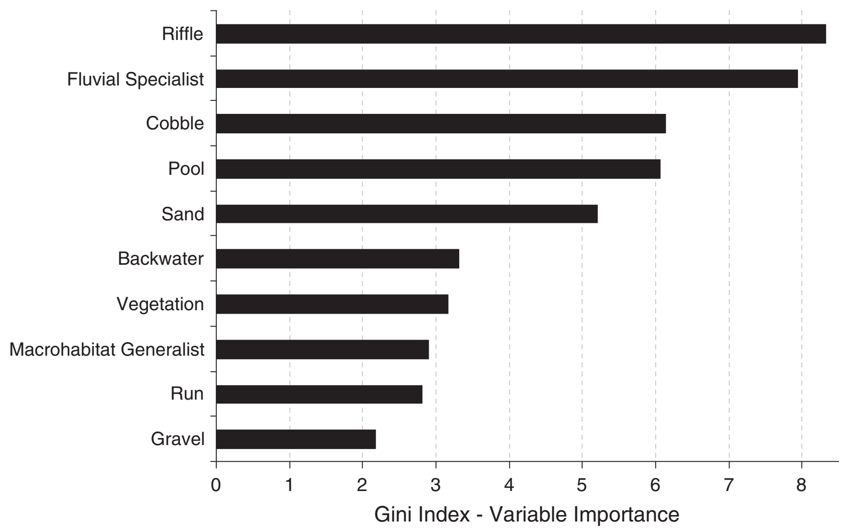

Figure 4. Variable importance plot of random forest Gini index values and fish habitat preference traits as predictors of streamflow variability.

assemblages at a large geographic scale. Carlisle *et al.* (2010) suggested that predictive model estimates of hydrological parameters likely underestimate the occurrence and severity of hydrological alteration because the estimates of expected values are derived from many reference sites (particularly in the Midwest) influenced by some anthropogenic disturbance. Thus, measures of deviation from expected streamflow variability may be conservative relative to pristine or pre-settlement hydrologic conditions. By using O_{cv}/E_{cv} values of 1.25 and 0.75 as eastwide criteria, in effect, we judged that a 25% change in streamflow variability was sufficient to classify a site to be in altered streamflow variability condition. The 10th and 90th percentile threshold values based on hydrological reference sites were used solely to standardize comparisons and should not be considered standards for regulatory purposes.

Results of this study indicate that the loss of expected native fish species was associated with reduced streamflow variability across a wide range of environmental settings found in the eastern USA. Reduced streamflow variability was related to a 35% loss in native fish species richness, on average. Poff *et al.* (1997) noted that many rivers no longer support native fish species as a consequence of changes in streamflow patterns. Haslouer *et al.* (2005) reported that hydrologic alteration poses a serious risk for the future of native fish species in Kansas. Those authors suggested that declines in minnow species uniquely adapted to Kansas rivers have been most dramatic since the 1950s, following a period of increased construction of mainstem reservoirs and other water-retention structures. Poff *et al.* (2007) suggested that alteration of high and low flows and thus altered streamflow variability has a continental-scale effect of

Table II. Kruskal–Wallis analyses, including χ^2 statistics and p values, and median per cent of predicted loss of expected native fish species with specific habitat preference traits at sites with reduced and unaltered streamflow variability

Habitat preference trait	Median %		χ^2	p value
	Reduced	Unaltered		
Riffle	59.5	0.0	33.47	0.001
Pool	25.3	0.0	29.95	0.001
Fluvial specialist	69.8	0.0	29.68	0.001
Cobble	12.4	0.5	22.49	0.001
Sand	32.6	0.0	22.31	0.001
Run	26.8	0.0	17.55	0.001
Backwater	36.1	0.0	16.22	0.001
Macrohabitat generalist	19.1	0.0	9.62	0.002
Gravel	18.2	0.0	9.28	0.002
Vegetation	19.1	0.0	9.14	0.002

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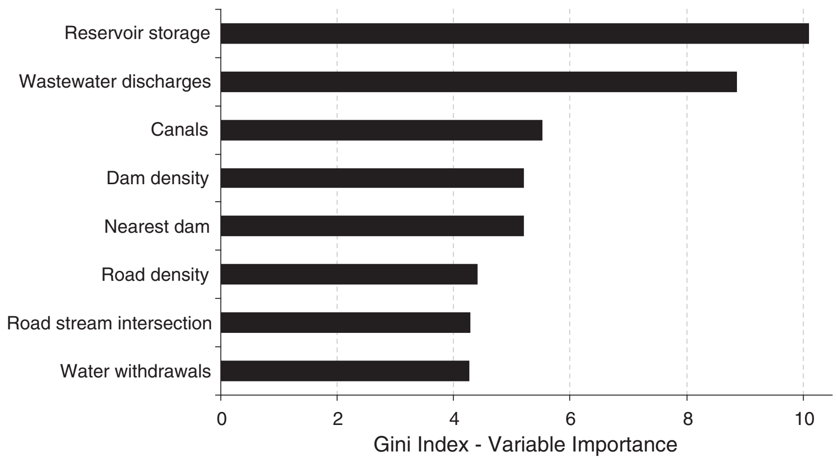

Figure 5. Variable importance plot of random forest Gini index values and factors that influence stream hydrology as predictors of streamflow variability.

homogenizing regionally distinct aquatic fauna, creating conditions that result in a loss of native biota.

The ecological significance of reduced streamflow variability was also suggested by our finding that the likelihood of fish assemblage impairment increased as the severity of reduced streamflow variability increased. The sensitivity of fish assemblages to reduced streamflow variability was indicated by a >50% probability of impairment fish assemblages associated with relatively low reductions of streamflow variability (<10%). We emphasize that our findings apply to a limited number of sites and range of alteration severities. In addition, other physical and chemical factors may be associated with streamflow alteration that may contribute to an increase in the probability of the occurrence of impaired fish assemblages (Bunn and Arthington, 2002). However, the relatively weak correlations between reduced streamflow variability and potential physicochemical covariates indicate that across divergent natural and anthropogenic settings, fish assemblage impairment is strongly associated with the severity of reduced streamflow variability.

Variation in the functional traits of native fish assemblages could be used to predict classes streamflow variability across the range of environmental settings found in the eastern USA. In particular, the loss of native fish species with preferences for riffle habitats and native fluvial-specialist species were important predictors of streamflow variability. Reduced streamflow variability was associated with a >50% loss of species with specific preferences for riffle and flowing-water habitats. Poff and Allan (1995) noted strong associations between functional-trait characteristics of fish and hydrological regimes at a regional scale. In a study of 34 sites in Wisconsin and Minnesota, Poff and Allan (1995) reported that fish species that preferred fast-flowing stream environments also tended to be silt-intolerant species and were associated with streams with a high predictability of streamflow. Meador and Carlisle (2009) reported that species with preferences for riffle habitats tended to occur less frequently than expected in the eastern USA, and the authors suggested that the loss of these species may be associated with reduced access to lotic habitats and sedimentation of coarser particle substrates.

Table III. Kruskal–Wallis analyses, including χ^2 statistics and p values, median values of selected factors that influence stream hydrology at sites with unaltered and reduced streamflow variability

Stream hydrology factor	Median		χ^2	*p* value
	Reduced	Unaltered		
Reservoir storage	68.1	3.0	27.53	0.001
Wastewater discharges	0.11	0.0	20.08	0.001
Canals	0.4	0.0	18.50	0.001
Nearest dam	116	112	6.30	0.012
Road density	1.8	1.6	3.98	0.046
Dam density	1.3	0.9	3.45	0.063
Water withdrawals	30 104	20 123	2.32	0.128
Road–stream intersections	0.64	0.69	0.05	0.829

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Alterations to hydrologic regimes that reduce natural flushing flows can result in the deposition of fine substrate particles between coarser streambed particles (Poff *et al.*, 1997). In the absence of the flushing flows, fish that are more sensitive to sedimentation can suffer higher mortality or migrate from the area (Poff *et al.*, 1997). Herbert and Gelwick (2003) suggested that streamflow variability associated with a reservoir in Texas may restrict movement of fluvial-specialist species and thus the ability to locate these habitats where they occur. Therefore, altered streamflow variability may not only be related to a loss of fluvial-specialist species at a site-specific scale but may affect the distribution of fluvial-specialist species throughout a basin by inhibiting fish movement. Perkin and Bonner (2010) noted that impoundments can alter streamflow variability through a reduction in downstream flood frequency, disrupting the structure and function of stream fish assemblages as evidenced by a loss of fluvial specialists. Perkin and Bonner (2010) suggested that the loss of fluvial specialists as a result of altered streamflow variability occurs through numerous mechanisms in addition to barriers to dispersion, including a loss of spawning cues and reproductive success.

Eastwide, factors that influence stream hydrology were important predictors of streamflow variability, particularly reservoir storage. Watershed hydrology in the east is influenced by hydrologic management focused primarily on flood control (Magilligan and Nislow, 2005). This is most often achieved through the management of small impoundments or large reservoirs that remove flood peaks and release the water later during normally low-flow periods, which would result in diminished maximum flows and inflated minimum flows. Reductions in peak flows and increases in minimum flows would result in reduced streamflow variabilities. In a study of the downstream effects of a Texas reservoir, Chang and Crowley (1997) reported that reduced high flows and enhanced low flows resulted in a 29% reduction in streamflow variability compared with pre-impoundment data.

Wastewater discharges also appeared to be an important predictor of streamflow variability. Of the 97 sites, 61 (62.9%) had at least one major permitted discharge source. Rivers and streams dominated by discharge effluents are typically located in the arid and semi-arid portions of the western USA (Hur *et al.*, 2007). However, Hur *et al.* (2007) reported that effluent flow rates for wastewater treatment plants along Reedy River, South Carolina, contributed as much as 51% of the streamflow in the main channel during low-flow periods. Thus, wastewater discharges in the eastern USA may significantly increase streamflow during typical low-flow periods, thereby reducing streamflow variability compared with what would be expected under minimally disturbed conditions.

Understanding relations between fish assemblages and streamflow alteration is critical to decisions regarding consumptive water use and the well-being of aquatic ecosystems (Postel and Richter, 2003). The results of this study provide quantitative evidence of links between hydrologic modifications, increasing the severity of reduced streamflow variability and the loss of native fish species, particularly species with preferences for flowing-water habitats. Poff (2009) noted that natural streamflow variability is critical to the long-term health and viability of aquatic assemblages and advocated that water resource managers should adopt a paradigm of natural streamflow variability as essential to sustainable ecosystem management. Developing understanding of natural streamflow variability has begun to influence reservoir operations that can be optimally managed to support ecologically relevant flow dynamism rather than a fixed regulatory minimum flow and still meet flood control and power operation needs (Dittman *et al.*, 2009; Suen *et al.*, 2009). However, management and conservation of streams will require careful consideration of natural streamflow variation and potential factors contributing to altered streamflow within the entire watershed to limit the loss of critical stream habitats and fish species uniquely adapted to live in those habitats.

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