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Flow alteration-ecology relationships in Ozark Highland streams: Consequences for fish, crayfish and macroinvertebrate assemblages☆



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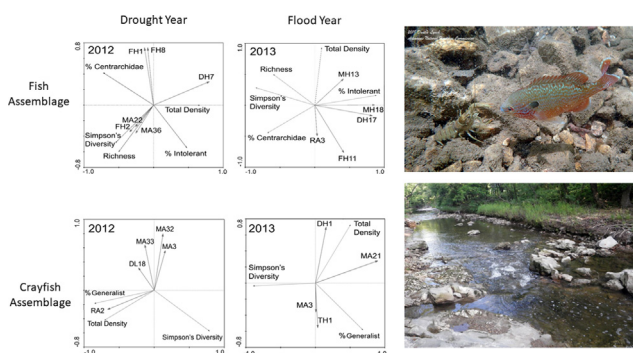
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HIGHLIGHTS

- Flow alteration-ecological response relationships vary temporally.
- Relationships also vary between taxonomic assemblages within the same community.
- Flow magnitude and frequency are the categories of alteration that affect most taxa.
- The majority of important flow metrics are altered relative to expected values.
- Effective conservation of stream communities depends on complex suite of variables.

GRAPHICAL ABSTRACT



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ABSTRACT

We examined flow alteration-ecology relationships in benthic macroinvertebrate, fish, and crayfish assemblages in Ozark Highland streams, USA, over two years with contrasting environmental conditions, a drought year (2012) and a flood year (2013). We hypothesized that: 1) there would be temporal variation in flow alteration-ecology relationships between the two years, 2) flow alteration-ecology relationships would be stronger during the drought year vs the flood year, and 3) fish assemblages would show the strongest relationships with flow alteration. We used a quantitative richest-targeted habitat (RTH) method and a qualitative multi-habitat (QMH) method to collect macroinvertebrates at 16 USGS gaged sites during both years. We used backpack electrofishing to sample fish and crayfish at 17 sites in 2012 and 11 sites in 2013. We used redundancy analysis to relate biological response metrics, including richness, diversity, density, and community-based metrics, to flow alteration. We found temporal variation in flow alteration-ecology relationships for all taxa, and that relationships differed greatly between assemblages. We found relationships were stronger for macroinvertebrates during the drought year but not for other assemblages, and that fish assemblage relationships were not stronger than the invertebrate taxa. Magnitude of average flow, frequency of high flow, magnitude of high flow, and duration of high flow were the most important categories of flow alteration metrics across taxa. Alteration of high and average flows was more important than alteration of low flows. Of 32 important flow alteration metrics across years and assemblages, 19 were significantly altered relative to expected values. Ecological responses differed substantially between drought and flood years, and this is likely to be exacerbated with predicted climate

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change scenarios. Differences in flow alteration–ecology relationships among taxonomic groups and temporal variation in relationships illustrate that a complex suite of variables should be considered for effective conservation of stream communities related to flow alteration.

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1. Introduction

The natural flow regime paradigm posits that the ecological integrity of rivers depends on their natural dynamic character (Poff et al., 1997), and that traditional approaches to managing streams by simply focusing on minimum low flows may be inadequate to protect these ecosystems and their biota (Bunn and Arthington, 2002; Poff et al., 2010). A concept related to the natural flow regime is the environmental flow regime; the key difference is that environmental flow regimes allow for some degree of hydrologic alteration in an attempt to balance the needs of humans as well as stream ecosystems, while still resulting in the same patterns and ecological outcomes as the natural flow regime (Poff et al., 1997; Bunn and Arthington, 2002; Poff et al., 2010). One of the great challenges in the implementation of the environmental flows (e-flows) approach to management and restoration is accounting for natural variability and complexity among different types of streams, even those within the same geographic region (Arthington et al., 2006; Kennard et al., 2010; Poff et al., 2010).

Natural streamflow regimes are threatened worldwide by a host of anthropogenic factors, including construction of dams and diversion structures, groundwater withdrawals from aquifers, and other hydromorphological alterations (Sondergaard and Jeppesen, 2007; Carlisle et al., 2010). Additionally, extreme climate events are expected to increase as a result of global climatic change, including many events that directly impact lotic ecosystems, such as increases in drought frequency, duration, and intensity in many regions of the world (Beniston et al., 2007; Beche et al., 2009), including in the focal region of this study, where these phenomena have already had consequences for rare and imperiled aquatic species (Magoulick and Lynch, 2015). The potential interactive effects of natural and anthropogenic stressors such as drought, climate change, and human water use on ecosystems highlight the need for increased understanding of each stressor (Christensen et al., 2006; Beche et al., 2009). For example, water withdrawals during dry years can reduce habitat connectivity and result in critical flow reductions (Beche et al., 2009). The maintenance of natural hydrologic regimes can also provide resistance to species invasion (Closs and Lake, 1996; Caiola et al., 2014), another pervasive world-wide phenomenon in freshwater habitats, often facilitated by anthropogenic alteration of flow regimes (Bunn and Arthington, 2002). For example, naturally flashy streams or rivers typified by frequent or rapid onset of high flows can prevent the establishment of non-native fish species that lack behavioral adaptations to rapid onset of flows (Meffe, 1984; Poff et al., 2010) or have a vulnerable juvenile stage present during periods of peak flows (Fausch et al., 2001; Poff et al., 2010).

Quantifying flow alteration, the degree of variation away from the natural flow regime, is a crucial step in environmental-flows based management approaches such as the ELOHA framework (Poff et al., 2010; Kendy et al., 2012; Gillespie et al., 2014; McManamay and Frimpong, 2015; King et al., 2015; Sengupta et al., 2018). While there is strong evidence that flow alteration generally negatively affects biodiversity as well as ecosystem function (Bunn and Arthington, 2002; Harris and Heathwaite, 2011; Warfe et al., 2014), there are challenges to establishing transferable relationships between flow alteration and ecological response (Poff and Zimmerman, 2010). Crucial steps in the ELOHA process include regional flow regime classification and the quantification of flow alteration; these steps are often made difficult by lack of hydrological data due to the somewhat sparse nature of

stream gages, which are often placed only on larger order stream segments and may not represent all stream types in an area (Zimmerman et al., 2018). Determining quantifiable relationships between hydrologic alteration and biological data is not only of great interest in informing management decisions relating to issues of water conservation and restoration (McManamay et al., 2014), but could potentially also be a critical tool in the assessment of the possible impacts of climate change on stream ecosystems and organisms (Xenopolous et al., 2005; Farjad et al., 2015).

The objective of this study was to examine flow alteration–biological response relationships for fish, crayfish, and benthic macroinvertebrate assemblages in the Ozark Highlands. We hypothesized that: 1) there would be temporal variation in flow alteration–ecology relationships between the two years (drought year versus flood year), 2) flow alteration–ecology relationships would be stronger during the drought year vs the flood year, and 3) fish assemblages would show the strongest relationships with flow alteration.

We hypothesized that the potential interactive effects between the dual stressors of drought and flow alteration would lead to stronger relationships during the drought year (Acuna et al., 2005; Beche et al., 2009; Bunn and Arthington, 2002; Dodds et al., 2004; Poff and Allan, 1995; Lynch et al., 2018). We hypothesized that fish would be more strongly impacted by drought than the other groups due to the ability of benthic macroinvertebrates and crayfish to utilize the hyporheic zone as a refuge (DiStefano et al., 2009; Wood et al., 2010; Stubbington, 2012) or to utilize drought-coping life history strategies ranging from aestivation (Wickson et al., 2012) and desiccation-resistant eggs (Pallares et al., 2016) to overland escape (Chester et al., 2014) or shifts in timing of emergence (Stenroth et al., 2010). To address our objectives, we conducted aquatic community sampling at 18 sites in Groundwater Flashy streams in the Ozark Highlands over two years and used redundancy analysis (RDA) to relate biological response variables to metrics of flow alteration, including magnitude, frequency, duration, timing, and rate of change.

1.1. Study area

The Ozark Highlands ecoregion of southern Missouri, northern Arkansas, and northeast Oklahoma, USA (Omernik and Griffith, 2014), is heavily affected by a suite of anthropogenic impacts, including rapid development of urban areas and agricultural practices that affect water quality (Petersen et al., 2005; Haggard, 2010; Scott et al., 2011), expansion of natural gas extraction (Johnson et al., 2015), displacement of native fauna due to the spread of invasive species (Magoulick and DiStefano, 2007; Larson et al., 2009), and direct hydrologic alteration of streams via construction of reservoirs and dams (TNC-OEAT, 2003). This region is home to a diverse assortment of freshwater habitats and aquatic species, including endemic fish, crayfish, mussels, macroinvertebrates, and herpetofauna (TNC-OEAT, 2003). Understanding the impacts of hydrologic alteration could be a crucial step in the formulation of guidelines for protection and restoration of stream ecosystems in the region.

2. Methods

2.1. Site selection

Sampling was conducted at 18 sites with USGS stream gages over two summer field seasons (May–July) during 2012 and 2013 in northwest

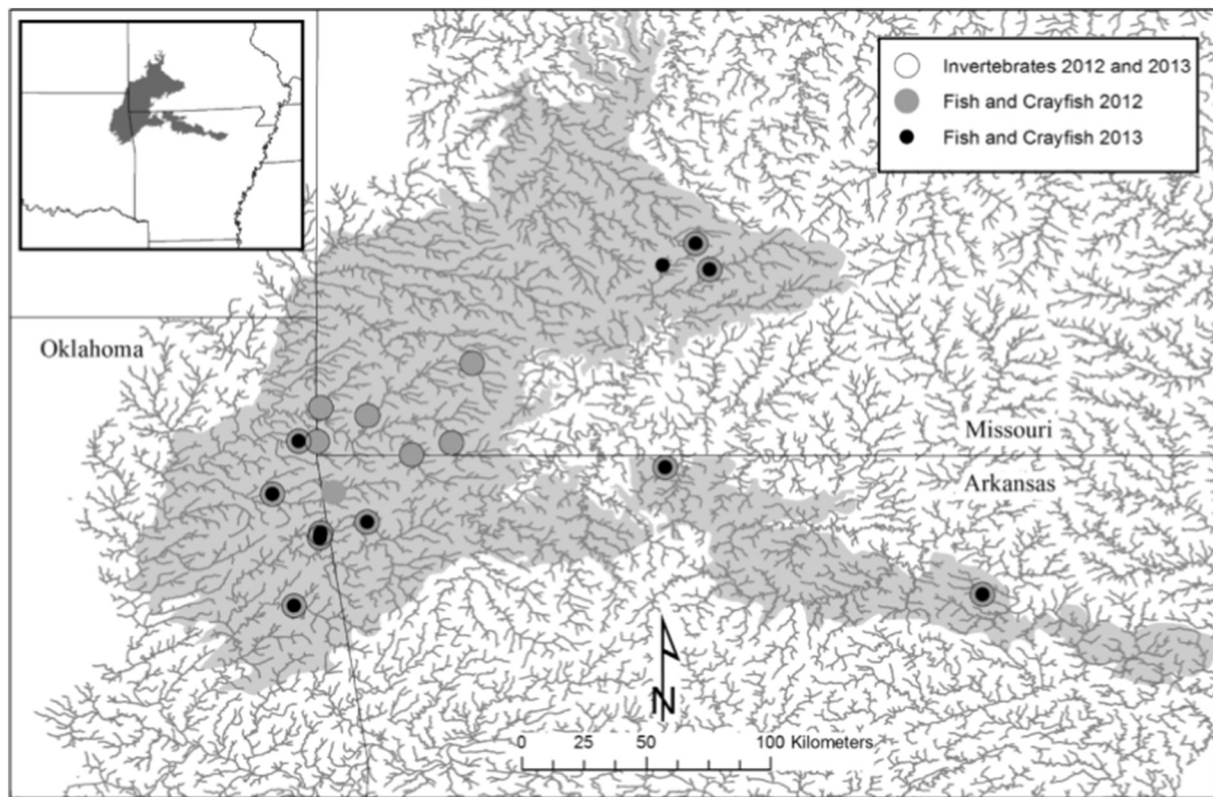


Fig. 1. Map of study area showing sample sites, stream network, and Springfield Plateau (shaded area).

Arkansas, southwest Missouri, and northeast Oklahoma (Fig. 1). Precipitation and flow conditions contrasted strongly between the two years. In summer 2012 the study area experienced an extreme drought, as measured on the Palmer Drought Severity Index (Palmer, 1965), while sustained higher than normal precipitation resulted in summer flooding at most sites during 2013 (NOAA, 2015). To facilitate biological comparisons, site selection was limited to a single ecoregion, the Ozark Highlands, a single physiographic region, the Springfield Plateau, and a single flow regime, Groundwater Flashy streams, based on a classification of Ozark-Ouachita Interior Highland streams into seven different hydrologic flow regimes (Leasure et al., 2016). Streams selected ranged in drainage area from 16 to 542 km².

Macroinvertebrate collections were taken at 16 sites that were the same in both years (Fig. 1). Due to extreme differences in sampling conditions between the two years (drought in 2012 versus extensive flooding in 2013), we were unable to resample seven of the largest sites from the first field season for fish and crayfish during the second season, but did add one additional site. Seventeen sites were sampled for fish and crayfish in 2012 and 11 in 2013, with 10 overlapping sites between the two years (Fig. 1).

2.2. Hydrologic variable and flow alteration estimation

We identified 64 USGS gaged streams in our study area in least-disturbed reference condition based on a composite hydrologic disturbance index (Falcone et al., 2010) using water withdrawals, density of major dams, change in dam storage between 1950 and 2009, percent canals in the watershed, water discharge locations, road density, and land cover fragmentation (Leasure et al., 2016). All streams selected in least-disturbed condition had an index less than the median of all gaged streams in the study area (Leasure et al., 2016). Using these streams, we developed a set of random forest models to predict 171 flow metrics (Olden and Poff, 2003). Full models were built initially that included 282 predictor variables describing climate, geology, soils,

topography, groundwater and landscape characteristics within reference watersheds (Appendix A). Importance of each variable was assessed using the default method of the *randomForest* R package (Liaw and Wiener, 2002) that is based on how much prediction error increases when each variable is permuted while others are left the same. A benefit of using random forest models for this approach is that they are not sensitive to the number of variables at each node or the number of trees (Liaw and Wiener, 2002). A reduced model was built for each flow metric that included only the 30 most important predictor variables.

Data were collected at all 208 USGS gages in the Interior Highlands for any predictor variable selected for at least one of the reduced random forest models. The reduced random forest models were used to predict values of each flow metric expected under natural conditions, as well as the distribution of expected values. The expected value for each flow metric under natural conditions was taken as the median of the predicted distribution.

Flow metrics were calculated for every complete 15 year period within the daily flow records of 18 gages used in this study. Flow alteration was calculated as:

$$\text{flow alteration} = \frac{\text{observed} - \text{median}(\text{predicted})}{\text{std.dev}(\text{predicted})}$$

where *observed* is the value of the flow metric from a specific period with a gage's record, and *predicted* is the distribution of values expected under natural conditions predicted by the random forest models. The standard deviation (*std. dev*) of predicted natural values was used for standardization rather than the interquartile range because the interquartile range may be zero for random forest models with high accuracy. We decided not to assess flow alteration as *observed/expected* as recommended by Carlisle et al. (2010) because of issues arising when expected values are zero. We dropped flow metrics that were outside

our threshold criteria for bias, precision and accuracy, reducing our initial set of 171 metrics to 154 (Appendix B).

2.3. Aquatic community assessment

Benthic macroinvertebrates, fish, and crayfish were sampled at each site. Reaches were defined by the presence of at least three discrete units of riffles, runs, and pools, and a qualitative attempt was made to ensure that sampling reaches were as comparable as possible between sites. Sampling was stratified by habitat to include three units each of riffles, runs and pools for a total of nine units per reach. Total area of reaches ranged from 140 to 957 m² and units averaged 8.3 m (SD = 3.2) in length across all habitat types. Habitat units were located at least 100 m from road crossings to avoid the hydrologic influence of man-made structures that could affect stream habitat (Barbour et al., 1999).

Benthic macroinvertebrate samples were typically collected at sites a few hours prior to fish and crayfish sampling. Macroinvertebrates were sampled using two different, complementary methods at each site, a semi-quantitative richest-targeted habitat (RTH) method and a qualitative multiple habitat (QMH) method, both developed for the U.S. Geological Survey National Water Quality Assessment (NAWQA) program (Moulton et al., 2002). Quantitative RTH collections were taken in riffles using a 500- μ m mesh Slack sampler (50 cm \times 30 cm) equipped with a 0.25 m² area PVC frame attached to the upstream end of the sampler (Moulton et al., 2002). The Slack sampler was positioned immediately downstream of the chosen quadrat perpendicular to the direction of flow. Large cobble and woody debris were lightly brushed, inspected for any remaining invertebrates, and then removed from the sampling area. The sampling area was then agitated by disturbing the substrate upstream of the mouth of the sampler, allowing the dislodged invertebrates to flow into the trailing net. The nine discrete subsamples were composited into a 19-L plastic bucket for processing, which consisted of rinsing and removing large debris from the samples, followed by elutriation and sieving (with a 500 μ m sieve) in order to separate invertebrates and organic debris from inorganic material.

The QMH method was used to document invertebrate taxa present in all habitat types throughout the reach (Moulton et al., 2002). Crew members assessed the entire reach to determine the number of different instream habitat types present and to estimate the proportion of each type. QMH samples were collected using a D-frame kicknet with 500- μ m mesh. Each habitat type was sampled in proportion to total habitat area for a standardized time of 1 h per reach. Samples were processed in the field as described for the RTH method.

In the laboratory, RTH and QMH samples were sorted on a square gridded subsampling frame of 25 5 \times 5 cm squares using a fixed-count approach targeting a minimum of 300 organisms (Barbour et al., 1999; Moulton et al., 2000). After pouring the sample into the frame and allowing it to settle evenly, an initial inspection was performed to remove large and rare organisms likely to be missed during subsampling. A grid square was randomly selected and all organisms present were removed from the grid and processed. Subsampling proceeded in this fashion until a minimum of 300 organisms were counted, with the square in which the 300th organism was counted also fully processed. Macroinvertebrates were identified to the lowest practical taxonomic level, generally family or genus. To estimate total numbers of organisms, a laboratory subsampling correction factor was used (Moulton et al., 2000) in which the total number of grids was divided by the number of grids sorted during subsampling and multiplied by the number of organisms subsampled. Large and rare organisms taken from the sample as a whole were added to these numbers without a correction factor. These numbers were then used to calculate invertebrate community response metrics.

Fish and crayfish were collected using a Smith-Root Model LR-24 backpack-electrofishing unit which has been shown effective for fish

and crayfish sampling in Ozark streams (Rabeni et al., 1997; Dauwalter and Pert, 2003). Standard LR-24 settings for power output based on ambient stream conductivity were used. Prior to sampling, 1.6 cm² mesh block-nets were placed at the end of each habitat unit to prevent animals from escaping or biasing sampling data by moving from one unit to another. A four-person team conducted three upstream passes per habitat unit. Collections from all passes were kept in separate buckets until all passes were completed. Each pass was processed separately and all specimens were identified to species and released live back into the stream.

2.4. Biological response metric selection

Biological response metrics were calculated for macroinvertebrate, fish, and crayfish assemblages (Table 1). A subset of metrics considered most ecologically relevant was chosen based on published relationships and best professional judgment. The five macroinvertebrate response metrics chosen were: abundance; taxa richness; Simpson's diversity; percent contribution of individuals belonging to Orders Ephemeroptera, Plecoptera, and Trichoptera (EPT), taxa that are associated with undisturbed habitat and high water quality (Karr, 1991); and percent contribution of the family Chironomidae, considered a generally tolerant taxon predicted to increase in abundance with increasing levels of perturbation (Barbour et al., 1999). Response metrics calculated from RTH and QMH samples were analyzed separately.

For crayfish, the three response metrics chosen were: Simpson's diversity, total crayfish density (per volume sampled), and percent contribution of species designated as habitat generalists in an assessment of invasion risk of crayfish in the eastern United States (Larson and Olden, 2010). These are represented in our dataset by two species, *Faxonius neglectus neglectus* and *Faxonius virilis*. Species richness was not used as a community response metric for crayfish due to the generally low and relatively uniform richness across sites.

For fish, the five biological response metrics chosen were: species richness, Simpson's diversity, total fish density (per volume sampled), percent of total individuals belonging to Family Centrarchidae, and percent of total individuals belonging to species categorized as intolerant, i.e. sensitive to various environmental perturbation, in an Index of Biotic Integrity specifically developed for fish assemblages of the Ozark Highlands (Dauwalter et al., 2003). Percent Centrarchidae was chosen as a response metric because most Ozark centrarchids are ecologically tolerant habitat generalists (Dauwalter et al., 2003; Robison and Buchanan, 1988).

Table 1
Mean (\pm SE) values for biological response metrics.

Variable	2012	2013
RTH macroinvertebrate taxa richness	22 (\pm 1.48)	19 (\pm 1.09)
RTH macroinvertebrate Simpson's diversity	0.81 (\pm 0.03)	0.77 (\pm 0.02)
RTH macroinvertebrate % EPT	49.65 (\pm 4.93)	59.93 (\pm 4.65)
RTH macroinvertebrate % Chironomidae	9.31 (\pm 3.48)	11.54 (\pm 2.50)
RTH macroinvertebrate abundance	2568 (\pm 757.14)	4064 (\pm 809.97)
QMH macroinvertebrate taxa richness	25 (\pm 2.28)	27 (\pm 1.29)
QMH macroinvertebrate Simpson's diversity	0.73 (\pm 0.05)	0.85 (\pm 0.02)
QMH macroinvertebrate % EPT	22.67 (\pm 0.04)	33.94 (\pm 0.04)
QMH macroinvertebrate % Chironomidae	6.33 (\pm 0.03)	17.46 (\pm 2.94)
QMH macroinvertebrate abundance	2710 (\pm 799.82)	3292 (\pm 398.98)
Fish species richness	16 (\pm 0.94)	15 (\pm 1.15)
Fish Simpson's diversity	0.73 (\pm 0.03)	0.73 (\pm 0.04)
Fish % intolerant	70.35 (\pm 4.21)	71.56 (\pm 4.03)
Fish % Centrarchidae	2.68 (\pm 0.77)	5.08 (\pm 1.67)
Fish total density	11.66 (\pm 0.77)	11.73 (\pm 1.51)
Crayfish Simpson's diversity	0.20 (\pm 0.05)	0.32 (\pm 0.06)
Crayfish % extraregional	80.10 (\pm 8.34)	40.46 (\pm 11.07)
Crayfish total density	3.54 (\pm 1.05)	8.00 (\pm 2.66)

2.5. Data analysis

Redundancy analysis (RDA) was used to evaluate flow alteration-ecology relationships separately for assemblages and sampling years. RDA is a canonical ordination procedure that examines relationships among response variables and predictor variables in multivariate space (ter Braak, 1995). Linear model RDA's were appropriate because preliminary Detrended Correspondence Analyses (DCA) indicated that species gradient lengths were <1 standard deviation (ter Braak, 1995). We used forward selection in CANOCO 4.5 (ter Braak and Smilauer, 2002) to select flow alteration variables that were related to response metrics. We limited the flow alteration variables to those with lambda ≥ 0.7 after entry into the model.

Prior to RDA analysis, response variables were centered and standardized. Scaling of ordination scores was focused on inter-response variable correlations rather than inter-sample distances, and the response variable scores were standardized to prevent variables with large variances from disproportionately influencing ordination diagrams (ter Braak and Smilauer, 2002). Monte Carlo permutations were performed for each RDA to test the significance of the canonical axes together and

were then performed for each RDA to determine the overall importance of remaining environmental variables in influencing response variables. Analyses of response variable-flow alteration relationships were performed separately for each year, taxonomic assemblage and sampling type (for macroinvertebrates). All significant hydrologic alteration metrics are listed and defined in Table 2. Percent variance explained in assemblage-environment relationships was examined by comparing eigenvalues from RDA analysis in order to test our second and third hypotheses.

3. Results

3.1. RTH macroinvertebrates

In 2012, RTH macroinvertebrate response metrics were significantly related to alteration of DH18, TA3, and RA3 (RDA $p < 0.001$, Table 2, Fig. 2). RA3 was significantly reduced relative to expected values (Fig. 2). Diversity, richness, and percent EPT were all negatively related to alteration of TA3, while abundance and percent Chironomidae were

Table 2
Important hydrologic alteration metrics (Olden and Poff, 2003) used in RDA analysis for 2012 and 2013 with mean (\pm SE) values.

Code	Definition	Category	Mean (\pm SE)
2012 RTH macroinvertebrates			
DH18	High flow duration (upper threshold 3 times median flows)	Duration of high flows	-0.41 (\pm 0.22)
TA3	Seasonal predictability of flooding	Timing of average flows	1.20 (\pm 0.59)
RA3	Fall rate	Rate of change of average flows	-0.13 (\pm 0.05)
2013 RTH macroinvertebrates			
MA22	Mean November flows	Magnitude of average flows	-0.27 (\pm 0.05)
FH3	High flood pulse count (upper threshold 3 times median daily flow)	Frequency of high flows	-0.95 (\pm 0.24)
DH23	Flood duration (mean annual number of days that flow remains above threshold averaged over all years)	Duration of high flows	-0.27 (\pm 0.16)
TH2	Variability in Julian date of annual maximum	Timing of high flows	-1.06 (\pm 0.57)
2012 QMH macroinvertebrates			
MA12	Mean January flows	Magnitude of average flows	-0.16 (\pm 0.06)
ML12	Mean minimum December flows	Magnitude of low flows	0.13 (\pm 0.04)
MH3	Mean maximum March flows	Magnitude of high flows	-0.14 (\pm 0.06)
MH20	Specific mean annual maximum flows (maximum flows divided by catchment area)	Magnitude of high flows	0.01 (\pm 0.27)
FH11	Flood frequency (mean number of discrete flood events per year)	Frequency of high flows	-0.56 (\pm 0.32)
2013 QMH macroinvertebrates			
MA29	Variability in June flows	Magnitude of average flows	-0.74 (\pm 0.21)
MH17	High flow discharge	Magnitude of high flows	-0.58 (\pm 0.15)
FH4	High flood pulse count (upper threshold 7 times median daily flow)	Frequency of high flows	-0.72 (\pm 0.20)
FH5	Flood frequency (upper threshold times median flow over all years)	Frequency of high flows	1.08 (\pm 0.68)
DH23	Flood duration (mean annual number of days that flow remains above threshold averaged over all years)	Duration of high flows	-0.27 (\pm 0.16)
2012 fish			
MA22	Mean November flows	Magnitude of average flows	-0.29 (\pm 0.05)
MA36	Variability across monthly flows	Magnitude of average flows	-0.82 (\pm 0.14)
FH1	High flood pulse count (pulse defined as 75th percentile)	Frequency of high flows	-0.74 (\pm 0.31)
FH2	Variability in high flood pulse count	Frequency of high flows	-0.75 (\pm 0.30)
FH8	Flood frequency (25th percentile upper threshold)	Frequency of high flows	-0.73 (\pm 0.32)
DH7	Variability in annual maxima of 3 day mean daily discharge	Duration of high flows	-0.04 (\pm 0.12)
2013 fish			
MH13	Variability across maximum monthly flows	Magnitude of high flows	0.26 (\pm 0.38)
MH18	Variability across annual maximum flows	Magnitude of high flows	1.60 (\pm 1.00)
FH11	Flood frequency (mean number of discrete flood events per year)	Frequency of high flows	-0.18 (\pm 0.41)
DH17	High flow duration (upper threshold 1 times median flows)	Duration of high flows	-0.54 (\pm 0.69)
RA3	Fall rate	Rate of change of average flows	-0.11 (\pm 0.09)
2012 crayfish			
MA3	Variability in daily flows	Magnitude of average flows	-0.42 (\pm 0.26)
MA32	Variability in September flows	Magnitude of average flows	-0.51 (\pm 0.2)
MA33	Variability in October flows	Magnitude of average flows	-0.41 (\pm 0.19)
DL18	Number of zero-flow days	Duration of low flows	-0.18 (\pm 0.13)
RA2	Variability in rise rate	Rate of change of average flows	2.31 (\pm 0.38)
2013 crayfish			
MA3	Variability in daily flows	Magnitude of average flows	-0.85 (\pm 0.32)
MA21	Mean October flows	Magnitude of average flows	-0.01 (\pm 0.06)
DH1	Annual maxima of daily mean discharge	Duration of high flows	-0.24 (\pm 0.08)
TH1	Julian date of annual maximum	Timing of high flows	0.55 (\pm 0.22)

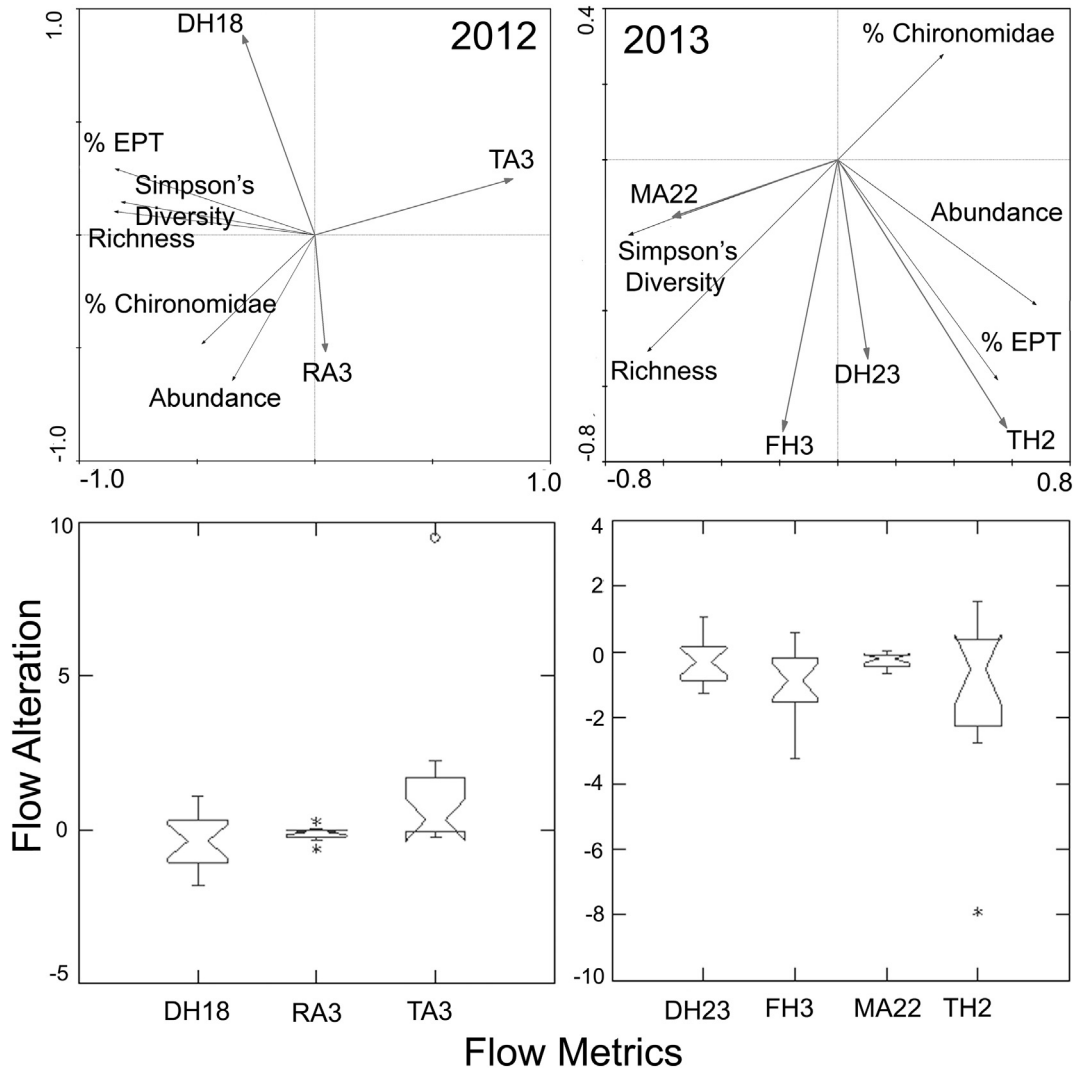


Fig. 2. Redundancy analysis ordination plot relating RTH (Richest Targeted Habitat) macroinvertebrate assemblages and selected flow alteration variables in 2012 and 2013. Boxplots show flow alteration variables used with notches indicating 95% CI. Angles of arrows indicate associations and length of arrows indicate strength of the relationship. Flow alteration variable abbreviations and descriptions are given in Table 2.

positively related to alteration of RA3 (Fig. 2). Cumulative percent variance explained by flow alteration was 88.6% for Axes 1 and 2 (Table 3).

In 2013, RTH macroinvertebrate assemblages were significantly related to alteration of MA22, FH3, DH23, and TH2 (RDA $p < 0.001$, Table 2, Fig. 2). MA22 and FH3 were significantly reduced relative to

expected values (Fig. 2). Diversity was positively related to alteration of MA22, while percent Chironomidae was negatively related to alteration of MA22 (Fig. 2). Percent EPT was positively related to alteration of TH2 (Fig. 2). Cumulative percent variance explained by flow alteration was 80.2% for Axes 1 and 2 (Table 3).

In RTH macroinvertebrate assemblages, no category of alteration metric stood out as most important. Of the seven important flow alteration metrics, two were duration, two were timing, one was magnitude, one was frequency, and one was rate of change (Table 2, Fig. 2). Four of seven metrics were high flow metrics, and the remaining three were average flow metrics. No metrics belonging to the low flow category were important. No metrics were important in RTH macroinvertebrate assemblages in both years. One metric, DH23, was also an important metric in QMH macroinvertebrate assemblages, and two others, MA22 and RA3, were also important metrics in fish assemblages (Table 2).

Table 3
Cumulative % variance in RDA axes.

Assemblage	Cumulative % variance explained	
	Axis 1	Axis 2
2012 (drought year)		
RTH macroinvertebrates	68.5	88.6
QMH macroinvertebrates	60.9	93.6
Fish	44.8	72.4
Crayfish	68.5	88.6
2013 (flood year)		
RTH macroinvertebrates	54.9	80.2
QMH macroinvertebrates	43.4	69.6
Fish	54.0	86.7
Crayfish	57.7	90.7

3.2. QMH macroinvertebrates

In 2012, QMH macroinvertebrate response metrics were significantly related to alteration of MA12, MH3, MH20, ML12, and FH11

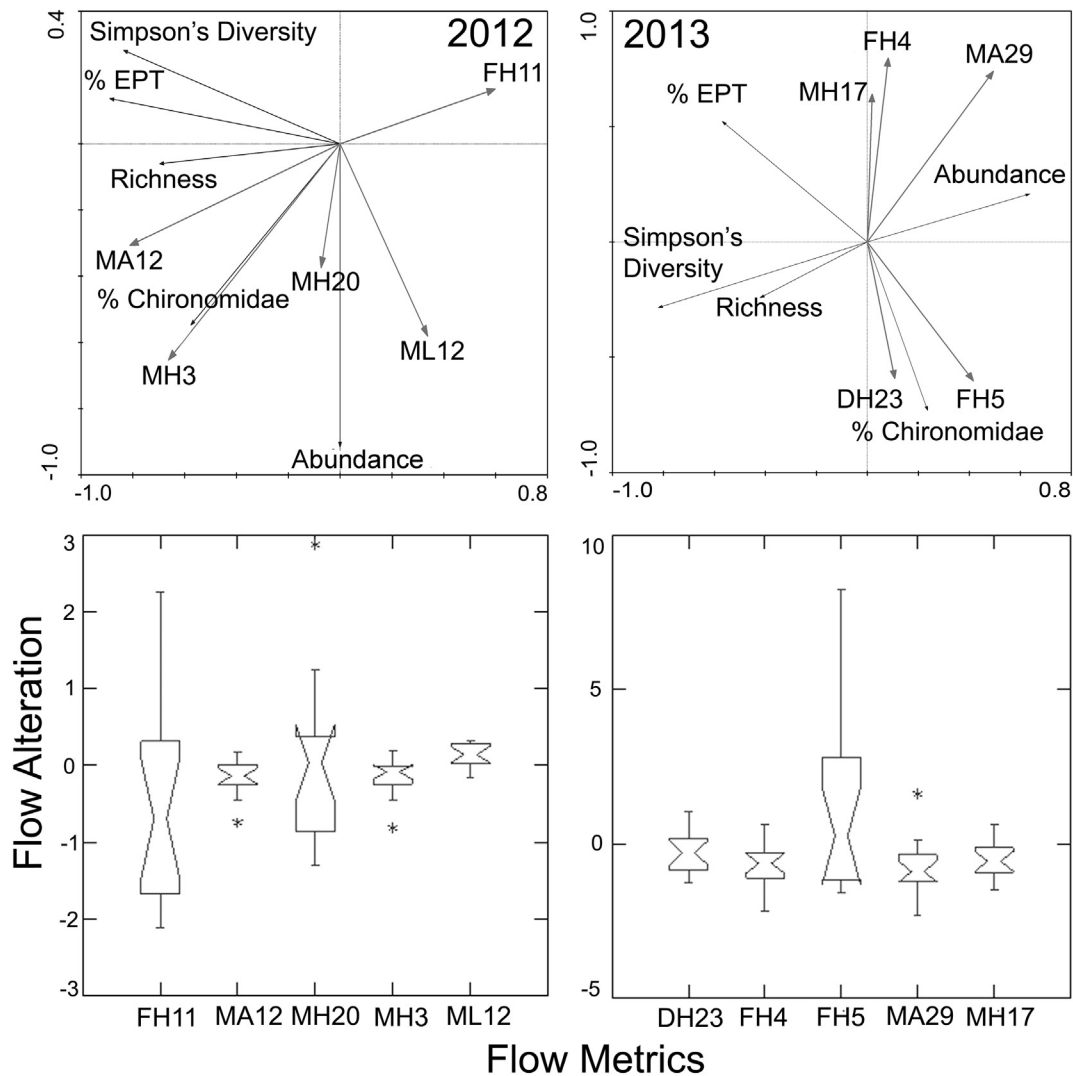


Fig. 3. Redundancy analysis ordination plot relating QMH (Qualitative Multi-Habitat) macroinvertebrate assemblages and selected flow alteration variables in 2012 and 2013. Boxplots show flow alteration variables used with notches indicating 95% CI. Angles of arrows indicate associations and length of arrows indicate strength of the relationship. Flow alteration variable abbreviations and descriptions are given in Table 2.

(RDA $p < 0.001$, Table 2, Fig. 3). MA12 and MH3 were significantly reduced and ML12 significantly increased relative to expected values (Fig. 3). Richness, diversity, and percent EPT were all negatively related to alteration of FH11, while percent Chironomidae was positively related to alteration of MH3 (Fig. 3). Cumulative percent variance explained by flow alteration was 93.6% for Axes 1 and 2 (Table 3).

In 2013, QMH macroinvertebrate response metrics were significantly related to alteration of MA29, MH17, FH4, FH5, and DH23 (RDA $p < 0.001$, Table 2, Fig. 3), and MA29, MH17, and FH4 were significantly reduced relative to expected values (Fig. 3). Percent EPT was negatively related to alteration of FH5 and DH23, while alteration of both of these metrics was positively related to percent Chironomidae (Fig. 3). Cumulative percent variance explained by flow alteration was 69.6% for Axes 1 and 2 (Table 3).

In QMH macroinvertebrate assemblages, magnitude was the most important category of alteration metric; six of the ten important alteration metrics belonged to this category (Table 2, Fig. 3). Frequency was the second most important category, with three of the ten. One metric belonged to the duration category. Seven of

the ten metrics were high flow metrics, with three average flow and one low flow. No metrics were important in QMH assemblages in both years. One metric, DH23, was also important in RTH macroinvertebrate assemblages, and another, FH11, in fish assemblages (Table 2).

3.3. Crayfish

In 2012, crayfish response metrics were significantly related to alteration of MA3, MA32, MA33, DL18 and RA2 (RDA $p < 0.001$, Table 2, Fig. 4). DL18, MA32, and MA33 were significantly reduced and RA2 significantly increased relative to expected values (Fig. 4). Diversity was negatively related to alteration of DL18, while total density and percent generalist crayfish were positively related to alteration of RA2 (Fig. 4). Cumulative percent variance explained by flow alteration was 88.6% for Axes 1 and 2 (Table 3).

In 2013, crayfish response metrics were significantly related to alteration of MA3, MA21, DH1, and TH1 (RDA $p < 0.001$, Table 2, Fig. 4). DH1 was significantly reduced and TH1 significantly increased relative to expected values (Fig. 4). Total

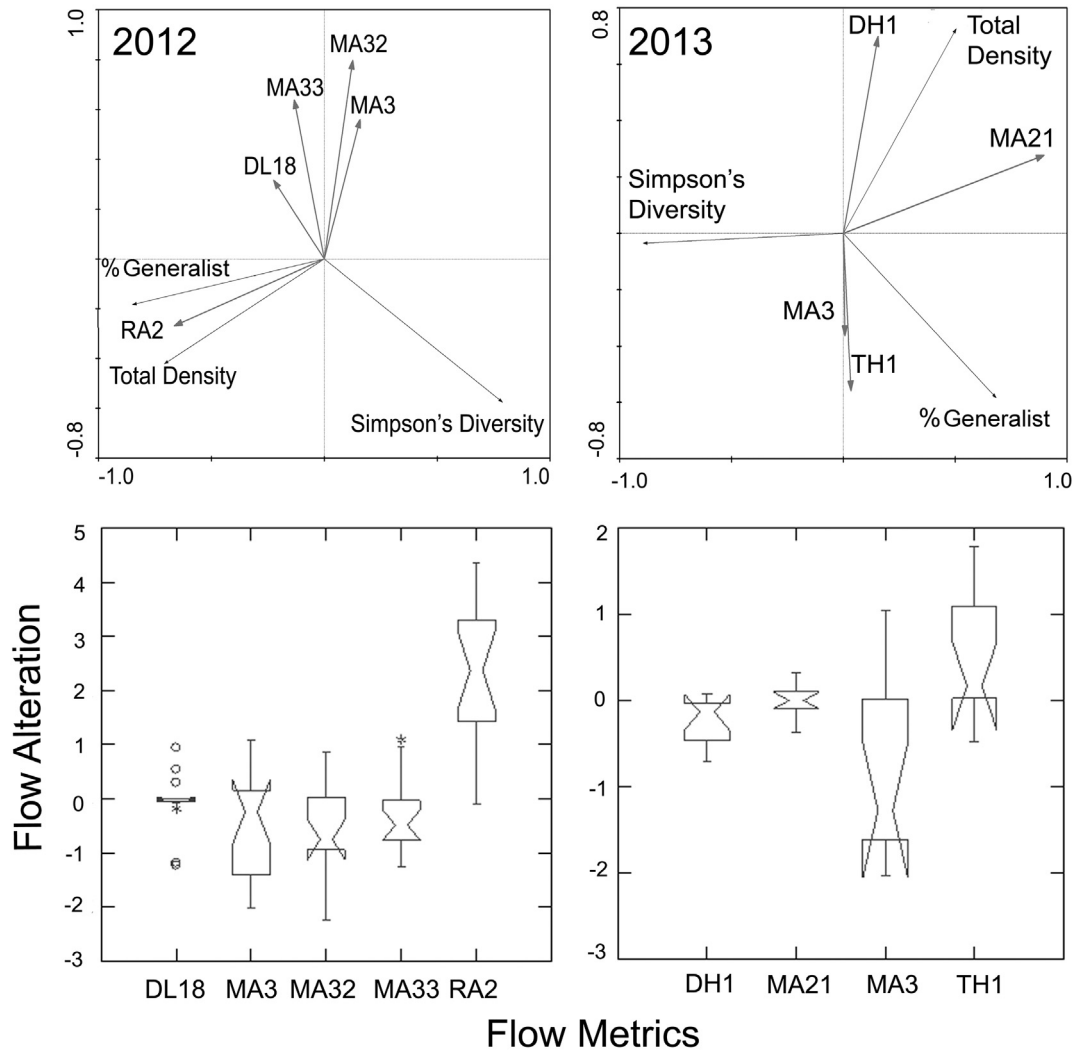


Fig. 4. Redundancy analysis ordination plot relating crayfish assemblages and selected flow alteration variables in 2012 and 2013. Boxplots show flow alteration variables used with notches indicating 95% CI. Angles of arrows indicate associations and length of arrows indicate strength of the relationship. Flow alteration variable abbreviations and descriptions are given in Table 2.

Density was positively related to alteration of DH1 while diversity was negatively related to alteration of MA21 (Fig. 4). Cumulative percent variance explained by flow alteration was 90.7% for Axes 1 and 2 (Table 3).

In crayfish assemblages, magnitude was the most important category of alteration metric; five of the nine important alteration metrics between years belonged to this category (Table 2, Fig. 4). Of the remaining four important metrics, two belonged to the duration category, one to the timing category, and one to the rate of change category. Six of the nine metrics were average flow metrics, with two high flows, and one low flow. One metric, MA3, was an important metric in crayfish assemblages in both years. No specific metrics important to crayfish assemblages were important in other taxonomic groups (Table 2).

3.4. Fish

In 2012, fish response metrics were significantly related to alteration of MA22, MA36, FH1, FH2, FH8, and DH7 (RDA $p < 0.001$, Table 2, Fig. 5). MA22, MA36, FH1, and FH2 were significantly reduced relative to expected values (Fig. 5). Diversity and richness were positively related to alteration of MA22, FH2, and MA36 and negatively related to alteration of DH7 (Fig. 4). Percent intolerant

fish was negatively related to alteration of FH1 and FH8 (Fig. 5). Cumulative percent variance explained by flow alteration was 72.4% for Axes 1 and 2 (Table 3).

In 2013, fish response metrics were significantly related to alteration of MH13, MH18, FH11, DH7, and RA3 (RDA $p < 0.001$, Table 2, Fig. 5). MH18 was significantly increased and RA3 significantly reduced relative to expected values (Fig. 5). Percent intolerant fish was positively related to alteration of MH18, total density negatively related to alteration of RA3, and richness and diversity negatively related to alteration of MH18 and DH7 (Fig. 5). Cumulative percent variance explained by flow alteration was 86.7% for Axes 1 and 2 (Table 3).

In fish assemblages, magnitude and frequency were the most important categories of flow alteration metrics; eight of the 11 important alteration metrics between years were in these two categories (Table 2, Fig. 5). Of the remaining three important metrics, two belonged to the duration category and one to the rate of change category. Eight of the 11 metrics were high flow metrics and the remaining three were in the average flow category. No metrics belonging to the low flow category were important. No metrics were important in fish assemblages in both years. MA22 and RA3 were also important metrics in RTH macroinvertebrate assemblages and FH11 in QMH macroinvertebrate assemblages (Table 2).

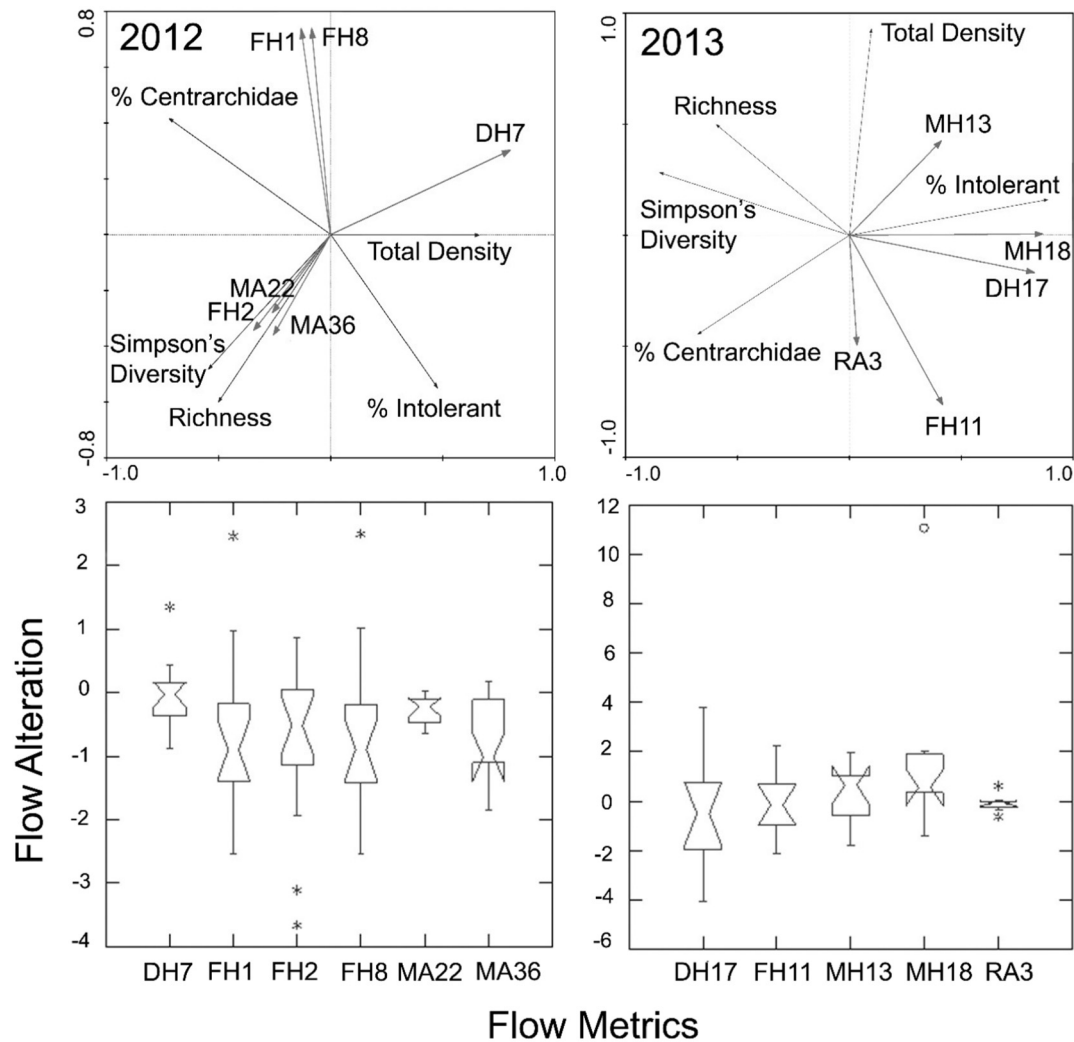


Fig. 5. Redundancy analysis ordination plot relating fish assemblages and selected flow alteration variables in 2012 and 2013. Boxplots show flow alteration variables used with notches indicating 95% CI. Angles of arrows indicate associations and length of arrows indicate strength of the relationship. Flow alteration variable abbreviations and descriptions are given in Table 2.

3.5. Aquatic community

Considering all four assemblages over both years, 32 different metrics of hydrologic alteration were significantly related to biological response metrics (Table 2). In order of importance, the five categories were ranked: magnitude (14), frequency (7), duration (6), timing (3) and rate of change (2). In terms of average, low, and high flows, metrics relating to alteration of high flows were the most numerous (19), followed by average flows (11), with a much lower number of important alteration metrics relating to low flows (2). All seven frequency metrics and all but one of the duration metrics were related to high flows, while the majority of important magnitude metrics were related to average flows. The four most important specific categories were MA (8), FH (7), MH (5), and DH (5). Four specific alteration metrics were important in multiple assemblages: MA22, FH11, DH23, and RA3 (Table 2).

4. Discussion

Our hypothesis that there would be temporal variation in flow alteration-ecology relationships was supported. The complete

overlap of sites for macroinvertebrate collections makes it possible to draw temporal comparisons in flow alteration-ecological response relationships between the two years for macroinvertebrate assemblages. The contrast between years was most pronounced in the RTH samples, which may be because they are collected only from riffles, the stream habitat most heavily affected by drought (Dekar and Magoulick, 2007; Chester and Robson, 2011). While we expected some differences between the years, it was still somewhat surprising to see no consistently important metrics between the two years in either RTH or QMH collections. In some cases, there were seemingly different relationships between response metrics. For example, RTH percent EPT was negatively related to alteration of TA3 (seasonal predictability of flooding) in 2012, whereas percent EPT was positively related to alteration of TH2 (variability in Julian date of annual maximum) in 2013. However, in both cases percent EPT was reduced with altered flow timing (discussed further below). It appears that alteration of flow timing is important for percent EPT, but specific relationships vary temporally.

Non-stationarity in environmental conditions can complicate our ability to formulate predictable flow-ecology relationships and pose challenges for the implementation of e-flows science (Poff et al., 2010; Rolls et al., 2012; Katz and Freeman, 2015; Poff, 2017; Lynch et al.,

2018). As the hydrologic cycle is further altered by global climate change and the severity, duration and frequency of droughts increases (Masson-Delmotte et al., 2013; Farjad et al., 2015) it is crucial to incorporate strategies that realistically account for these phenomena when implementing e-flows science into management decisions (Poff, 2017). One such strategy is to focus on resilience, the maintenance of processes and relationships that are robust and able to maintain integrity despite anticipated changes in environmental conditions (Poff, 2017; Mazor et al., 2018).

Our hypotheses that flow alteration-ecology relationships would be stronger during the drought year and that fish assemblages would show the strongest flow-alteration relationships, had much less support, and showed year- and taxa-dependent caveats. Relationship strength, as indicated by cumulative percent variance explained in Axes 1 and 2 of the RDA's, was greater during the drought year for benthic macroinvertebrate assemblages, but weaker for fish and crayfish, with the pattern reversed during the flood year. Fish assemblage relationships were stronger than macroinvertebrates and lower than crayfish during the flood year, but weaker than all other groups during the drought year. Overall, relationships were slightly stronger during the drought year than the flood year, and relationships were actually weaker in fish than in the macroinvertebrate assemblages.

With respect to which categories of alteration metrics were most important, the prominence of magnitude and frequency is of particular interest given that regional e-flows studies have suggested that magnitude of flow is an important influence on aquatic communities (Monk et al., 2006; Armstrong et al., 2011; Kendy et al., 2012), while others have found that frequency of floods may be one of the most important determinants of community structure in streams (Dodds et al., 2004; Matthews et al., 2013; Matthews et al., 2014). Anthropogenic alteration of streamflow magnitudes is a widespread phenomenon; in an assessment of 2888 streamflow monitoring sites throughout the conterminous U.S., Carlisle et al. (2010) found that streamflow magnitude was altered at 86% of assessed streams, and that diminished magnitudes were better predictors of biological integrity in both fish and macroinvertebrate assemblages than other physical and chemical covariates. Reduction in high flow frequencies has also been linked to a decrease in the ecological integrity of river systems (Ward and Stanford, 1995). The general trend in our study area in both magnitude and frequency metrics was towards reduction relative to expected values.

Compared to alteration of high and average flows, alteration of low flows appeared to be a considerably less important influence on biota in Groundwater Flashy streams in the Ozark Highlands; only two of 32 important metrics across years and assemblages were low flow related. Although both floods and droughts act as major hydrologic disturbances in stream ecosystems and can exert significant influence on biota (Lake, 2000), the alteration of low-flow hydrology has been relatively less studied than that of high flows (Rolls et al., 2012). In the present study, we focused on Groundwater Flashy streams, one of the most common flow regimes in the Ozark Highlands (Leasure et al., 2016), but it is likely that in other flow regimes, alteration of low flows may be more important. Different natural flow regimes within the same region may be more or less susceptible to particular forms of flow alteration, which is the reason that flow regime classification is a crucial step in the assessment of hydrologic alteration (Poff et al., 2010). The seven distinct flow regimes in the Ozark Highlands can be divided into three broad categories – groundwater, runoff, and intermittent streams (Leasure et al., 2016). Runoff and intermittent flow regimes are categorized by more frequent low flow spells and lower base flows than groundwater streams; it may be that low flow metrics play a greater role in the life history of biota in these streams and therefore alteration of those metrics would have greater

impact. Poff (1992) suggested that perennial runoff and intermittent streams may be more strongly affected by alteration of low flows and groundwater streams more affected by alteration of high flows; the latter at least appears to be reflected in the present study.

RTH macroinvertebrate assemblages differed in key ways from the others in this study. This was the only group in which magnitude was not the most important category of flow alteration metric. It was also the only assemblage in which no flow alteration category was clearly more prominent than the others. Predictability of flooding is thought to be critically important to macroinvertebrate assemblages. Fritz and Dodds (2005) found that streams with low flow predictability had consistently lower macroinvertebrate taxa richness than those with greater predictability. Alteration of the variability in high flow timing (TH2) was also related to both percent EPT taxa and abundance in 2013. Predictable timing of floods may be very important in aquatic macroinvertebrates that rely on life-history adaptations to avoid disturbances rather than escaping on a per-event basis, particularly taxa that require gill respiration as juveniles but have an aerial adult stage, e.g. EPT taxa (Lytle, 2008). In the present study, predictability of flooding (TA3) was altered towards higher predictability and was negatively related to all response variables in 2012. Likewise, alteration towards increased variability in high flow timing (TH2) was positively related to increased percent EPT taxa and abundance in 2013, but it is important to note that TH2 alteration ranges from strongly negative to slightly positive so percent EPT and abundance increased with less altered (i.e., more normal) TH2. Therefore, in both cases percent EPT was reduced with altered flow timing. It appears that alteration of flow timing, regardless of direction, may negatively influence RTH macroinvertebrate assemblages in these systems.

Unlike RTH assemblages, QMH assemblages showed a pattern consistent with fish and crayfish assemblages with respect to the prominence of magnitude alteration metrics. Interestingly, QMH assemblages show more of an affinity with fish than crayfish assemblages in terms of the importance of high flow frequency (FH). Relationships between response variables in the two years were more consistent in QMH than RTH samples. It is possible that the inclusion of pool and run habitats, which act as refuges for macroinvertebrates during summer drying (Chester and Robson, 2011), may have somewhat ameliorated the effects of drought in 2012 in QMH compared to RTH samples. Temporal variation in relationships was also apparent in QMH assemblages, however, as no individual flow alteration metrics were significant in both years. General trends among QMH macroinvertebrate assemblages in the region include reduction of important metrics relating to magnitude and variability in average and high flows, as well as frequency and duration of high flows. These may have a variety of effects on QMH macroinvertebrate assemblages in the region; in a few cases, some trends may actually offset each other. For example, decreasing magnitude of average flows (MA12) may lead to a decrease in richness which could be somewhat ameliorated by the trend towards decreasing flood frequency (FH11) (Fig. 3). Examining synergies and indirect effects of flow alteration on ecosystem structure and function could be a fruitful avenue for future research.

It should be noted that care should be taken in interpreting the flow alteration-ecology relationships because flow can be negatively or positively altered or unaltered. Therefore, negative alteration can be positively correlated with a response variable. For example, in Fig. 2 the alteration of FH3 is positively related to Taxa Richness and negatively related to %Chironomidae, but FH3 is negatively altered and high FH3 values are near normal (i.e., FH3 = 0). Therefore, Taxa Richness is greater and %Chironomidae is reduced when FH3 is near normal.

Magnitude alteration was the most important category in both crayfish and fish assemblages. The two strongly differ in one important way, however – the lack of any important frequency alteration metrics in crayfish assemblages. The ability of crayfish species in the region to more fully utilize the hyporheic zone during dry periods (DiStefano et al., 2009; Larson et al., 2009) may make them less dependent on frequent high flow events than fish assemblages; this may lessen the impact that alteration of flood frequency has on them. MA3, variability in daily flows, was a consistently important metric in crayfish assemblages in the region, as it was selected in both 2012 and 2013 despite a lack of overlap between sites. The relationship between alteration of flow variability and density was similar to that observed in fish assemblages in this study, i.e. the relationship between fish density and MA36 in 2012, and is also supported by previous studies of flow variability and fish density (Craven et al., 2010).

In fish assemblages, the association between richness and diversity and alteration of variability in both average flow magnitude (MA22 and MA36) and high flow frequency, (FH2) is supported by studies relating hydrologic variation to North American stream fishes (Ward, 1998; Niu et al., 2012, but see McGarvey, 2014). The trend towards reduction of these metrics in our study area could be associated with an overall decline in richness and diversity of stream fishes in the region. While previous studies have suggested that aquatic biodiversity is often lower in modified or disturbed streams than in those with relatively intact natural flow regimes (Ward and Stanford, 1995; Gehrke et al., 1999), it has been an ongoing challenge for stream ecologists to unravel the direct effects of flow alteration from multiple associated stressors that often accompany development in watersheds, e.g. land-use factors or declining water quality (Bunn and Arthington, 2002). Our study provides evidence that alteration of specific flow metrics can influence richness and diversity in stream biota.

Overall, our results show the importance of magnitude and high flow alteration to stream assemblages in these systems. However, patterns related to alteration of specific flow metrics between years or between taxa are less obvious. It is possible that redundancy between tested flow metrics used to explain similar ecological processes may be responsible for lack of patterns with specific flow metrics. Future research that builds on established flow alteration-biological response relationships in a way that specifically elucidates functional links would be worthwhile.

Another caveat to consider is that, while relationships appeared to vary between years, our ability to detect these relationships may have varied as well based on the very different sampling conditions between drought and flood years. Detection probability of freshwater fish can vary strongly between samples taken at different flow magnitudes, and this may influence inferences based on fish community-flow relationships (Pregler et al., 2015; Gwinn et al., 2016). Similar factors may affect detection probability in benthic macroinvertebrate assemblages (Meador et al., 2011; Wisniewski et al., 2013). Furthermore, while hydrology plays a major role in structuring aquatic assemblages, it is heavily interrelated to many other factors, including geomorphology, land-use, and water quality; the ecological effects of hydrologic alteration are best examined within the context of this suite of factors (Poff et al., 2006; McManamay and Frimpong, 2015; Lynch et al., 2018). Finally, while we examined flow alteration-ecology relationships in a predominant flow regime (Groundwater Flashy streams) in the Ozark Highlands, these relationships may strongly differ in other flow regimes even within the same ecoregion (Poff, 1992; Poff et al., 2010; Leasure et al., 2016). Future studies of flow alteration-ecology relationships focused on other flow regimes would help to form a more complete picture of the impact of hydrologic alteration on stream communities.

5. Conclusions

Flow alteration appears to be an important influence on community structure in Groundwater Flashy streams in the Ozark Highlands. The most important categories of alteration influencing stream biota were MA, FH, MH, and DH. The fact that three of these categories were high flow-related suggests the overall importance of high flows as a determinant of community structure and composition in these systems. Of the 32 important metrics across years and assemblages, 19 were significantly altered relative to expected values. General patterns, such as the importance of magnitude and high flow alteration, were apparent across assemblages and may be useful to managers and stakeholders attempting to conserve freshwater ecosystems in the region. However, key differences between taxonomic groups, as well as temporal variation in relationships, suggest that a complex suite of flow metrics should be considered for effective conservation of stream communities related to flow alteration. Environmental flows concepts are increasingly finding traction in regions across the world (Belmar et al., 2011; Buchanan et al., 2013; Rolls and Arthington, 2014; O'Brien et al., 2017; Zhang et al., 2012), but could be enhanced by a better understanding of complexity with respect to interactions between temporal variation, disturbance, and taxa-dependent response differences.

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Appendix A

Predictor variable	Spatial extent
Average base flow index	W, P
Average groundwater recharge	W, P
Maximum elevation	W
Maximum slope	W
Watershed ratio	W
Watershed area	W
Average stream slope	W, P
Density of upstream confluences	W
Count of upstream confluences	W
Spring density	W
Spring count	W
Percent coverage of shale	W
Percent coverage of dolostone	W
Coverage of shale	W
Coverage of dolostone	W
Percent coverage of Ozark Plateau aquifer	W

(continued)

Predictor variable	Spatial extent
Coverage of Ozark Plateau aquifer	W
Average bulk density	W, P
Average soil clay content	W, P
Subsurface flow contact time index	W, P
Average soil water capacity	W, P
Average water table depth	W, P
Average hydrologic group B	W, P
Average hydrologic group C	W, P
Average hydrologic group D	W, P
Infiltration-excess overland flow rates	W, P
Average soil K factor	W, P
Average soil organic matter	W, P
Average overland flow	W, P
Snow percent of total precipitation	W, P
Average soil fraction < 0.74 mm	W, P
Average soil fraction < 2 mm	W, P
Average soil fraction < 5 mm	W, P
Average soil permeability	W, P
Average annual potential evapotranspiration	W, P
Average rainfall and runoff factor	W, P
Average rock depth	W, P
Average percent sand	W, P
Average percent silt	W, P
Dominant surface geology	W, P
Average topographic wetness index	W, P
Percent coverage of limestone	W
Percent coverage of sand	W
Percent coverage of sandstone	W
Coverage of limestone	W
Coverage of sand	W
Coverage of sandstone	W
Canopy cover	W
Average elevation	W, P
Elevation range	W
Average slope	W, P
Isothermality	W, P
Maximum temperature of warmest month	W, P
Average diurnal temperature range	W, P
Average temperature coldest quarter	W, P
Average temperature driest quarter	W, P
Average temperature warmest quarter	W, P
Average temperature wettest quarter	W, P
Minimum temperature coldest month	W, P
Precipitation coldest quarter	W, P
Precipitation driest month	W, P
Precipitation driest quarter	W, P
Precipitation January	W, P
Precipitation February	W, P
Precipitation March	W, P
Precipitation April	W, P
Precipitation May	W, P
Precipitation June	W, P
Precipitation July	W, P
Precipitation August	W, P
Precipitation September	W, P
Precipitation October	W, P
Precipitation November	W, P
Precipitation December	W, P
Precipitation seasonality	W, P
Precipitation warmest quarter	W, P
Precipitation wettest month	W, P
Precipitation wettest quarter	W, P
Temperature annual range	W, P
Temperature seasonality	W, P
Average temperature January	W, P
Average temperature February	W, P
Average temperature March	W, P
Average temperature April	W, P
Average temperature May	W, P
Average temperature June	W, P
Average temperature July	W, P
Average temperature August	W, P
Average temperature September	W, P
Average temperature October	W, P
Average temperature November	W, P
Average temperature December	W, P

(continued)

Predictor variable	Spatial extent
Percent coverage of chert	W
Percent coverage of alluvial terrace	W
Percent coverage of alluvium	W
Coverage of chert	W
Coverage of alluvial terrace	W
Coverage of alluvium	W
Dominant geology	W, P
Coverage of forest in 1992	W
Coverage of wetlands in 1992	W
Percent coverage of forest in 1992	W
Percent coverage of wetlands in 1992	W
Percent coverage of deciduous forests in 1992	W
Percent coverage of evergreen forests in 1992	W
Percent coverage of mixed forests in 1992	W
Coverage of deciduous forests in 1992	W
Coverage of evergreen forests in 1992	W
Coverage of mixed forests in 1992	W
Dominant aspect	W, P
Average annual temperature	W, P
Annual precipitation	W, P
Maximum temperature January	W, P
Maximum temperature February	W, P
Maximum temperature March	W, P
Maximum temperature April	W, P
Maximum temperature May	W, P
Maximum temperature June	W, P
Maximum temperature July	W, P
Maximum temperature August	W, P
Maximum temperature September	W, P
Maximum temperature October	W, P
Maximum temperature November	W, P
Maximum temperature December	W, P
Minimum temperature January	W, P
Minimum temperature February	W, P
Minimum temperature March	W, P
Minimum temperature April	W, P
Minimum temperature May	W, P
Minimum temperature June	W, P
Minimum temperature July	W, P
Minimum temperature August	W, P
Minimum temperature September	W, P
Minimum temperature October	W, P
Minimum temperature November	W, P
Minimum temperature December	W, P
Minimum winter temperature	W, P
Dominant aquifer	W, P
Average annual runoff	W, P
Average runoff January	W, P
Average runoff February	W, P
Average runoff March	W, P
Average runoff April	W, P
Average runoff May	W, P
Average runoff June	W, P
Average runoff July	W, P
Average runoff August	W, P
Average runoff September	W, P
Average runoff October	W, P
Average runoff November	W, P
Average runoff December	W, P
Coverage of red clay	W
Coverage of cherty red clay	W
Coverage of loam	W
Coverage of sandy and stony colluvium	W
Coverage of floodplain and alluvium gravel terraces	W
Percent coverage of red clay	W
Percent coverage of cherty red clay	W
Percent coverage of loam	W
Percent coverage of sandy and stony colluvium	W
Percent coverage of floodplain and alluvium gravel terraces	W
Percent coverage of Edwards-Trinity aquifer	W
Coverage of Edwards-Trinity aquifer	W
Stream density	W
Stream length	W
Minimum elevation	W
Maximum stream slope	W
Strahler stream order	P
Shreve stream order	P

Flow metric	Definition	<i>n</i>	Unique	Shift	Bias	Bias (interquartile range)	Imprecision	Imprecision (interquartile range)	Absolute error	Absolute Error (interquartile range)	R ²	R ² (interquartile range)	Root mean square error	Normalized root mean square error
MA1	Mean daily flow	64	64	1	-0.07	-0.04	0.37	0.23	0.23	0.15	0.89	0.85	0.49	0.07
MA2	Median daily flow	64	57	1	-0.01	0.00	0.67	0.37	0.34	0.19	0.89	0.81	0.54	0.08
MA3	Coefficient of variation in daily flows	64	64	0	-5.47	-0.09	48.49	0.76	24.53	0.38	0.73	0.62	36.57	0.11
MA4	Coefficient of variation of the logs in daily flows corresponding to the	64	64	1	-0.02	-0.09	0.17	0.64	0.09	0.32	0.76	0.68	0.14	0.12
MA5	Mean daily flows divided by median daily flows	64	60	0	0.22	0.12	1.17	0.64	0.64	0.35	0.50	0.65	1.43	0.11
MA6	Ratio of 10th/90th percentiles in daily flows overall years	55	55	1	0.13	0.04	0.75	0.24	0.42	0.13	0.73	0.87	0.93	0.13
MA7	Ratio of 20th/80th percentiles in daily flows overall years	61	60	1	0.07	0.04	0.69	0.35	0.35	0.18	0.68	0.82	0.68	0.12
MA8	Ratio of 25th/75th percentiles in daily flows overall years	64	63	1	0.06	0.04	0.45	0.32	0.22	0.16	0.65	0.84	0.54	0.13
MA9	Ranges in daily flows (MA6) divided by median daily flows	64	60	0	0.43	0.10	2.33	0.53	1.13	0.26	0.45	0.74	3.87	0.10
MA10	Ranges in daily flows (MA7) divided by median daily flows	64	61	0	0.18	0.09	1.06	0.53	0.57	0.29	0.49	0.71	1.49	0.10
MA11	Ranges in daily flows (MA8) divided by median daily flows	64	59	0	0.10	0.07	0.76	0.53	0.40	0.28	0.52	0.72	0.93	0.11
MA12	Mean monthly flow for January	64	64	1	-0.10	-0.07	0.51	0.34	0.26	0.17	0.85	0.83	0.57	0.08
MA13	Mean monthly flow for February	64	64	1	-0.09	-0.06	0.48	0.31	0.25	0.16	0.87	0.84	0.54	0.08
MA14	Mean monthly flow for March	64	64	0	47.42	0.07	262.62	0.38	122.23	0.18	0.73	0.82	455.00	0.10
MA15	Mean monthly flow for April	64	64	1	-0.08	-0.05	0.38	0.25	0.21	0.14	0.90	0.86	0.47	0.07
MA16	Mean monthly flow for May	64	64	1	-0.12	-0.08	0.42	0.26	0.23	0.14	0.90	0.86	0.48	0.07
MA17	Mean monthly flow for June	64	64	0	30.07	0.09	86.92	0.25	60.73	0.17	0.78	0.83	304.41	0.08
MA18	Mean monthly flow for July	64	64	1	-0.07	-0.03	0.66	0.34	0.34	0.17	0.88	0.83	0.54	0.08
MA19	Mean monthly flow for August	64	64	1	0.01	0.01	0.61	0.33	0.29	0.16	0.90	0.84	0.53	0.07
MA20	Mean monthly flow for September	64	64	1	-0.03	-0.02	0.44	0.27	0.25	0.15	0.86	0.85	0.54	0.08
MA21	Mean monthly flow for October	64	64	1	-0.08	-0.05	0.45	0.27	0.26	0.15	0.84	0.85	0.60	0.09
MA22	Mean monthly flow for November	64	64	1	-0.06	-0.04	0.71	0.45	0.36	0.22	0.84	0.78	0.59	0.09
MA23	Mean monthly flow for December	64	64	1	-0.05	-0.03	0.63	0.41	0.33	0.22	0.84	0.78	0.59	0.09
MA24	Coefficient of variation in monthly flows for January	64	46	0	-0.08	0.00	24.64	0.52	12.17	0.26	0.67	0.74	20.39	0.14
MA25	Coefficient of variation in monthly flows for February	64	47	0	0.45	0.01	20.26	0.60	10.52	0.31	0.65	0.69	16.74	0.12
MA26	Coefficient of variation in monthly flows for March	64	46	0	1.25	0.03	20.67	0.54	10.69	0.28	0.68	0.72	16.32	0.14
MA27	Coefficient of variation in monthly flows for April	64	47	0	0.03	0.00	23.84	0.65	12.05	0.33	0.71	0.67	16.69	0.13
MA28	Coefficient of variation in monthly flows for May	64	53	0	1.73	0.04	23.53	0.49	11.75	0.24	0.75	0.76	19.58	0.12
MA29	Coefficient of variation in monthly flows for June	64	59	0	3.94	0.06	21.74	0.34	11.85	0.18	0.80	0.82	19.00	0.12
MA30	Coefficient of variation in monthly flows for July	64	54	0	5.23	0.07	26.17	0.34	17.29	0.22	0.72	0.78	33.25	0.11
MA31	Coefficient of variation in monthly flows for August	64	58	0	6.74	0.08	37.92	0.46	21.78	0.27	0.65	0.73	41.52	0.12
MA32	Coefficient of variation in monthly flows for September	64	55	0	4.98	0.05	36.49	0.40	19.53	0.21	0.69	0.79	37.43	0.13
MA33	Coefficient of variation in monthly flows for October	64	54	1	-0.03	-0.03	0.34	0.35	0.18	0.18	0.79	0.82	0.33	0.12
MA34	Coefficient of variation in monthly flows for November	64	49	1	-0.02	-0.03	0.21	0.36	0.11	0.18	0.81	0.82	0.20	0.10
MA35	Coefficient of variation in monthly flows for December	64	53	0	-0.78	-0.01	20.40	0.32	9.85	0.16	0.74	0.84	20.59	0.11
MA36	Variability in monthly flows divided by median monthly flows, where variability is calculated as range	64	63	0	1.01	0.14	4.15	0.57	2.31	0.32	0.55	0.68	5.20	0.11
MA37	Variability in monthly flows divided by median monthly flows, where variability is calculated as interquartile	64	56	0	0.03	0.04	0.62	0.71	0.30	0.34	0.51	0.66	0.68	0.10
MA38	Variability in monthly flows divided by median monthly flows, where variability is calculated as 90th-10th percentile	64	61	1	-0.04	-0.12	0.23	0.67	0.10	0.29	0.63	0.71	0.19	0.11
MA39	Coefficient of variation in mean monthly flows	64	63	0	0.18	0.01	16.61	0.81	7.64	0.37	0.62	0.63	12.54	0.13
MA40	(Mean monthly flow—median monthly flow)/median monthly flow	64	51	1	-0.01	-0.02	0.16	0.64	0.08	0.34	0.55	0.66	0.16	0.11
MA41	Mean annual flow divided by catchment area	64	53	1	0.00	-0.01	0.07	0.33	0.04	0.19	0.71	0.81	0.09	0.10
MA42	Variability in annual flows divided by median annual flows, where variability is calculated as range	64	46	0	-0.05	-0.09	0.51	1.00	0.25	0.49	0.38	0.51	0.35	0.15
MA43	Variability in annual flows divided by median annual flows, where variability is calculated as interquartile	64	38	1	0.00	-0.04	0.10	0.93	0.05	0.48	0.35	0.52	0.09	0.18
MA44	Variability in annual flows divided by median annual flows, where variability is calculated as 90th-10th percentile	64	45	1	0.00	0.01	0.12	0.84	0.06	0.43	0.45	0.57	0.10	0.15
MA45	(Mean annual flow—median annual flow)/median annual flow	64	21	0	0.00	0.05	0.06	1.14	0.03	0.59	0.23	0.41	0.06	0.15
ML1	Mean minimum monthly flow for January	64	64	1	-0.02	-0.02	0.64	0.39	0.32	0.20	0.90	0.80	0.51	0.07
ML2	Mean minimum monthly flow for February	64	64	1	-0.04	-0.03	0.57	0.34	0.31	0.18	0.90	0.82	0.50	0.07

ML3	Mean minimum monthly flow for March	64	64	0	17.87	0.08	66.64	0.31	34.52	0.16	0.81	0.84	180.01	0.08
ML4	Mean minimum monthly flow for April	64	64	0	25.87	0.10	74.42	0.29	40.73	0.16	0.81	0.84	204.79	0.08
ML5	Mean minimum monthly flow for May	64	63	1	0.00	0.00	0.55	0.27	0.30	0.15	0.92	0.85	0.49	0.07
ML6	Mean minimum monthly flow for June	64	64	1	-0.05	-0.02	0.64	0.27	0.33	0.14	0.91	0.86	0.56	0.08
ML7	Mean minimum monthly flow for July	64	62	1	0.03	0.01	1.02	0.41	0.44	0.18	0.89	0.82	0.63	0.09
ML8	Mean minimum monthly flow for August	64	63	1	0.04	0.02	0.95	0.38	0.47	0.19	0.89	0.81	0.67	0.09
ML9	Mean minimum monthly flow for September	64	64	1	0.12	0.05	0.95	0.40	0.46	0.19	0.88	0.81	0.66	0.09
ML10	Mean minimum monthly flow for October	64	63	1	0.11	0.05	0.84	0.37	0.42	0.18	0.88	0.82	0.61	0.09
ML11	Mean minimum monthly flow for November	64	64	1	0.02	0.01	0.73	0.41	0.36	0.20	0.88	0.80	0.57	0.08
ML12	Mean minimum monthly flow for December	64	64	1	0.00	0.00	0.73	0.44	0.35	0.21	0.88	0.79	0.55	0.08
ML13	Coefficient of variation in minimum monthly flows	64	64	0	-0.85	-0.02	18.97	0.42	9.53	0.21	0.66	0.79	19.51	0.15
ML14	Mean of the lowest annual daily flow divided by median annual daily flow averaged across all years	61	29	0	0.00	0.01	0.06	0.24	0.03	0.12	0.79	0.88	0.09	0.15
ML15	Mean of the lowest annual daily flow divided by mean annual daily flow averaged across all years	64	21	1	0.00	0.03	0.02	0.22	0.02	0.16	0.78	0.84	0.05	0.14
ML16	Median of the lowest annual daily flows divided by median annual daily flows averaged across all years	61	26	0	0.01	0.02	0.06	0.25	0.03	0.14	0.77	0.86	0.09	0.15
ML17	Seven-day minimum flow divided by mean annual daily flows averaged across all years	64	25	1	0.01	0.05	0.03	0.22	0.02	0.15	0.78	0.85	0.05	0.14
ML18	Coefficient of variation in ML17	63	63	1	0.04	0.02	0.39	0.27	0.20	0.14	0.65	0.86	0.49	0.18
ML19	Mean of the ratio of the lowest annual daily flow to the mean annual daily flow times 100 averaged across all years	64	59	1	0.02	0.01	0.67	0.29	0.34	0.15	0.78	0.85	0.61	0.16
ML20	Ratio of base flow volume to total flow volume	64	36	1	0.00	0.02	0.07	0.55	0.04	0.29	0.81	0.71	0.05	0.11
ML21	Coefficient of variation in annual minimum flows averaged across all years	63	63	0	5.30	0.03	54.01	0.35	27.62	0.18	0.55	0.82	78.27	0.17
ML22	Mean annual minimum flows divided by catchment area	64	21	0	0.01	0.09	0.04	0.44	0.02	0.21	0.71	0.79	0.07	0.13
MH1	Mean of the maximum monthly flows for January	64	64	0	293.63	0.12	988.71	0.40	622.04	0.25	0.67	0.75	1395.83	0.12
MH2	Mean of the maximum monthly flows for February	64	64	0	191.50	0.07	1047.22	0.38	506.52	0.18	0.72	0.82	1400.17	0.11
MH3	Mean of the maximum monthly flows for March	64	64	0	262.33	0.07	1095.46	0.31	687.51	0.20	0.71	0.80	1744.35	0.12
MH4	Mean of the maximum monthly flows for April	64	64	0	437.31	0.12	1201.51	0.33	780.70	0.21	0.73	0.79	1995.83	0.11
MH5	Mean of the maximum monthly flows for May	64	64	0	328.69	0.09	1242.02	0.35	711.69	0.20	0.70	0.80	2066.25	0.12
MH6	Mean of the maximum monthly flows for June	64	64	0	193.09	0.10	844.68	0.42	456.29	0.22	0.66	0.78	1084.08	0.10
MH7	Mean of the maximum monthly flows for July	64	64	1	-0.02	-0.01	0.70	0.47	0.37	0.25	0.79	0.75	0.59	0.10
MH8	Mean of the maximum monthly flows for August	64	64	1	-0.10	-0.05	0.54	0.29	0.29	0.15	0.82	0.85	0.62	0.08
MH9	Mean of the maximum monthly flows for September	64	64	0	125.20	0.14	376.81	0.42	232.67	0.26	0.50	0.74	592.78	0.11
MH10	Mean of the maximum monthly flows for October	64	64	1	-0.11	-0.08	0.74	0.52	0.40	0.28	0.71	0.72	0.79	0.11
MH11	Mean of the maximum monthly flows for November	64	64	1	-0.09	-0.07	0.85	0.63	0.43	0.32	0.77	0.68	0.64	0.10
MH12	Mean of the maximum monthly flows for December	64	64	0	515.04	0.18	1292.24	0.46	737.29	0.26	0.65	0.74	1340.80	0.15
MH13	Coefficient of variation in mean maximum monthly flows	64	63	1	0.01	0.07	0.11	0.73	0.06	0.38	0.39	0.62	0.10	0.16
MH14	Median of the highest annual daily flow divided by the median annual daily flow averaged across all years	64	62	0	8.46	0.14	38.64	0.64	21.18	0.35	0.60	0.65	42.39	0.14
MH15	Mean of the 1st percentile from the flow duration curve divided by median daily flow across all years	64	64	0	3.50	0.11	21.94	0.70	11.56	0.37	0.55	0.63	23.19	0.13
MH16	Mean of the 10th percentile from the flow duration curve divided by median daily flow across all years	64	62	0	0.21	0.05	2.20	0.53	1.14	0.27	0.44	0.73	3.83	0.10
MH17	Mean of the 25th percentile from the flow duration curve divided by median daily flow across all years	64	54	0	0.09	0.09	0.61	0.55	0.33	0.30	0.49	0.70	0.85	0.11
MH18	Coefficient of variation of logarithmic annual maximum flows	64	60	0	0.36	0.13	1.48	0.56	0.79	0.29	0.45	0.71	1.66	0.18
MH19	Skewness in annual maximum flows	64	54	2.62	0.00	-0.01	0.22	0.98	0.10	0.46	0.05	0.54	0.22	0.19
MH20	Mean annual maximum flows divided by catchment area	64	63	0	1.28	0.05	10.37	0.38	5.18	0.19	0.77	0.81	8.15	0.11
MH21	Mean of the high flow volume (calculated as the area between the hydrograph and the upper threshold during the high flow event) divided by median annual daily flow across all years. The upper threshold is defined as median annual flow	64	64	0	13.01	0.12	60.95	0.57	26.49	0.25	0.27	0.75	101.61	0.12
MH22	Mean of the high flow volume (calculated as the area between the hydrograph and the upper threshold during the high flow event) divided by median annual daily flow across all years. The upper threshold is defined as 3 times median annual flow	64	64	1	0.00	0.00	0.55	0.71	0.28	0.36	0.62	0.64	0.46	0.12
MH23	Mean of the high flow volume (calculated as the area between the hydrograph and the upper threshold during the high flow event) divided by median annual daily flow across all years. The upper threshold is defined as 7 times median annual flow	64	64	0	1.84	0.04	31.77	0.73	16.49	0.38	0.31	0.62	58.49	0.11
MH24	Mean of the high peak flow during the high flow event (defined by the upper	64	63	0	1.93	0.11	12.88	0.72	6.83	0.38	0.56	0.62	12.86	0.16

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Flow metric	Definition	n	Unique	Shift	Bias	Bias (interquartile range)	Imprecision	Imprecision (interquartile range)	Absolute error	Absolute Error (interquartile range)	R ²	R ² (interquartile range)	Root mean square error	Normalized root mean square error
MH25	threshold) divided by median annual daily flow. The upper threshold is defined as median annual flow Mean of the high peak flow during the high flow event (defined by the upper threshold) divided by median annual daily flow. The upper threshold is defined as 3 times median annual flow	64	64	0	2.22	0.12	10.41	0.58	6.11	0.34	0.56	0.66	12.64	0.16
MH26	Mean of the high peak flow during the high flow event (defined by the upper threshold) divided by median annual daily flow. The upper threshold is defined as 7 times median annual flow	64	62	1	0.00	0.00	0.33	0.68	0.17	0.34	0.65	0.66	0.27	0.14
MH27	See MH24–26, where the upper threshold is defined as the 25th percentile from the flow duration curve	64	64	0	2.15	0.12	11.42	0.65	6.18	0.35	0.54	0.65	14.04	0.16
FL1	Number of annual occurrences during which the magnitude of flow remains below a lower threshold. Hydrologic pulses are defined as those periods within a year in which the flow drops below the 25th percentile (low pulse) of all daily values for the time period	64	59	1	-0.01	-0.04	0.17	0.60	0.09	0.30	0.40	0.70	0.15	0.19
FL2	Coefficient of variation in FL1	64	64	0	0.26	0.02	9.24	0.76	5.27	0.43	0.58	0.57	7.72	0.14
FL3	Total number of low flow spells (threshold equal to 5% of mean daily flow) divided by the record length in years	64	51	0	1.17	0.01	28.21	0.28	15.31	0.15	0.71	0.85	27.09	0.16
FH1	See FL1, where the high pulse is defined as the 75th percentile	64	62	1	-0.01	-0.02	0.14	0.48	0.07	0.25	0.70	0.75	0.12	0.12
FH2	Coefficient of variation in FH1	64	64	0	-0.18	-0.02	5.77	0.61	3.15	0.33	0.50	0.67	4.99	0.15
FH3	See FH1, where the upper threshold is defined as 3 times median daily flow, and the value is represented as an average instead of a tabulated count	64	64	0	-2.06	-0.07	19.38	0.66	9.67	0.33	0.70	0.67	14.59	0.12
FH4	See FH1, where the upper threshold is defined as 7 times median daily flow, and the value is represented as an average instead of a tabulated count	64	63	0	-0.86	-0.03	13.42	0.54	6.58	0.27	0.67	0.73	11.09	0.11
FH5	Mean number of high flow events per year using an upper threshold of median flow over all years	64	56	0	-0.10	-0.04	1.34	0.58	0.69	0.30	0.44	0.70	1.17	0.15
FH6	Mean number of high flow events per year using an upper threshold of 3 times median flow over all years	64	64	0	0.02	0.01	1.61	0.57	0.83	0.30	0.66	0.70	1.38	0.12
FH7	Mean number of high flow events per year using an upper threshold of 7 times median flow over all years	64	64	0	-0.06	-0.01	1.88	0.44	0.97	0.23	0.76	0.77	1.57	0.12
FH8	See FH5–7, where the 25th percentile is used as the upper threshold	64	62	1	-0.01	-0.02	0.14	0.49	0.07	0.26	0.69	0.74	0.12	0.12
FH9	See FH5–7, where the 75th percentile is used as the upper threshold	64	54	0	0.08	0.05	1.02	0.63	0.51	0.31	0.43	0.69	0.93	0.19
FH10	See FH5–7, where the median of the annual minima is used as the upper threshold	64	51	1	0.05	0.15	0.18	0.60	0.10	0.32	0.32	0.68	0.18	0.17
FH11	Mean number of discrete flood events per year	64	30	1	0.00	0.02	0.07	0.78	0.04	0.38	0.10	0.62	0.06	0.22
DL1	Annual minima of mean of daily discharge	64	61	1	0.13	0.04	1.15	0.40	0.53	0.18	0.88	0.82	0.71	0.10
DL2	Annual minima of 3-day mean of daily discharge	64	60	1	0.14	0.05	0.97	0.34	0.51	0.17	0.88	0.83	0.70	0.10
DL3	Annual minima of 7-day mean of daily discharge	64	63	1	0.13	0.05	1.01	0.35	0.51	0.18	0.88	0.82	0.69	0.10
DL4	Annual minima of 30-day mean of daily discharge	64	62	1	0.07	0.03	0.99	0.38	0.50	0.19	0.88	0.81	0.68	0.09
DL5	Annual minima of 90-day mean of daily discharge	64	64	1	0.06	0.04	0.70	0.42	0.39	0.23	0.89	0.77	0.54	0.08
DL6	Coefficient of variation in mean of daily discharge	61	61	0	5.39	0.04	48.75	0.32	25.22	0.17	0.55	0.83	70.26	0.19
DL7	Coefficient of variation in 3-day mean of daily discharge	61	61	0	7.93	0.05	51.51	0.35	25.23	0.17	0.54	0.83	72.15	0.18
DL8	Coefficient of variation in 7-day mean of daily discharge	62	62	0	8.26	0.06	47.76	0.33	22.69	0.16	0.53	0.84	66.61	0.18
DL9	Coefficient of variation in 30-day mean of daily discharge	63	63	0	4.02	0.03	37.73	0.30	21.96	0.17	0.64	0.83	46.65	0.17
DL10	Coefficient of variation in 90-day mean of daily discharge	64	64	1	-0.04	-0.04	0.38	0.39	0.23	0.23	0.68	0.77	0.34	0.14
DL11	Mean annual 1-day minimum, divided by median flow	64	33	0	0.01	0.02	0.07	0.29	0.04	0.15	0.76	0.85	0.09	0.15
DL12	Mean annual 7-day minimum, divided by median flow	64	30	1	0.01	0.03	0.07	0.30	0.04	0.15	0.75	0.85	0.08	0.16
DL13	Mean annual 30-day minimum, divided by median flow	64	33	0	0.00	0.01	0.11	0.34	0.06	0.17	0.76	0.83	0.10	0.15
DL14	Mean magnitude of flows exceeded 75% of the time (calculated from the flow duration curve) divided by median daily flow, overall years	64	41	1	0.00	-0.01	0.09	0.35	0.05	0.18	0.73	0.82	0.08	0.16
DL15	Mean magnitude of flows exceeded 90% of the time (calculated from the flow duration curve) divided by median daily flow, overall years	64	32	0	0.01	0.03	0.10	0.32	0.05	0.16	0.75	0.84	0.10	0.16
DL16	Mean duration of FL1	64	62	1	0.01	0.02	0.24	0.62	0.10	0.27	0.42	0.73	0.19	0.18
DL17	Coefficient of variation in DL16	64	63	0	-1.69	-0.08	15.10	0.75	7.58	0.37	0.16	0.63	12.97	0.20
DL18	Mean annual number of days having zero daily flow	64	32	1	0.02	0.01	0.82	0.31	0.43	0.16	0.62	0.84	0.96	0.21
DL19	Coefficient of variation in DL18	64	33	1	0.06	0.01	1.28	0.25	0.62	0.12	0.62	0.88	1.61	0.27

DL20	Percentage of all months with zero flow	64	18	1	0.03	0.01	0.57	0.27	0.32	0.15	0.50	0.85	0.86	0.24
DH1	Annual maxima of mean of daily discharge	64	64	1	-0.06	-0.04	0.52	0.41	0.28	0.22	0.85	0.78	0.49	0.09
DH2	Annual maxima of 3-day mean of daily discharge	64	64	0	598.82	0.09	1963.84	0.31	1119.05	0.17	0.69	0.83	3333.27	0.10
DH3	Annual maxima of 7-day mean of daily discharge	64	64	1	-0.10	-0.07	0.49	0.35	0.23	0.17	0.87	0.83	0.51	0.08
DH4	Annual maxima of 30-day mean of daily discharge	64	64	0	103.87	0.07	465.67	0.30	266.65	0.17	0.68	0.83	1040.77	0.10
DH5	Annual maxima of 90-day mean of daily discharge	64	64	0	61.35	0.06	292.05	0.29	152.40	0.15	0.72	0.85	598.47	0.10
DH6	Coefficient of variation in annual maxima of mean daily discharge	64	62	1	0.00	-0.01	0.21	0.78	0.10	0.38	0.18	0.62	0.20	0.18
DH7	Coefficient of variation in annual maxima of 3-day mean of daily discharge	64	62	1	0.01	0.03	0.19	0.79	0.09	0.40	0.21	0.60	0.18	0.15
DH8	Coefficient of variation in annual maxima of 7-day mean of daily discharge	64	63	1	0.01	0.03	0.15	0.60	0.07	0.28	0.30	0.72	0.17	0.14
DH9	Coefficient of variation in annual maxima of 30-day mean of daily discharge	64	64	0	-0.04	0.00	8.15	0.68	4.15	0.35	0.46	0.65	6.66	0.16
DH10	Coefficient of variation in annual maxima of 90-day mean of daily discharge	64	63	0	0.00	0.00	7.07	0.61	3.46	0.30	0.55	0.70	5.68	0.14
DH11	Mean annual 1-day maximum, divided by median flow	64	63	0	11.05	0.12	58.90	0.66	29.43	0.33	0.63	0.67	52.95	0.14
DH12	Mean annual 7-day maximum, divided by median flow	64	64	0	1.51	0.06	18.25	0.78	8.49	0.36	0.50	0.64	18.51	0.12
DH13	Mean annual 30-day maximum, divided by median flow	64	63	0	0.46	0.05	6.44	0.67	3.40	0.36	0.46	0.64	7.41	0.11
DH14	Monthly flow equalled or exceeded 95% of the time divided by mean monthly flow	64	52	0	0.00	0.00	0.35	0.71	0.17	0.36	0.63	0.64	0.27	0.14
DH15	Mean duration of FH1	64	61	0	0.32	0.13	1.67	0.68	0.92	0.38	0.56	0.62	1.23	0.15
DH16	Coefficient of variation in DH15	64	64	1	-0.01	-0.02	0.24	0.61	0.12	0.30	0.56	0.70	0.23	0.13
DH17	See DH15, where the upper threshold is defined as 1 times median flows, and the value is represented as an average instead of a tabulated count	64	64	1	0.03	0.08	0.22	0.68	0.11	0.35	0.46	0.65	0.18	0.13
DH18	See DH15, where the upper threshold is defined as 3 times median flows, and the value is represented as an average instead of a tabulated count	64	62	0	0.31	0.09	2.53	0.71	1.35	0.38	0.23	0.62	3.03	0.15
DH19	See DH15, where the upper threshold is defined as 7 times median flows, and the value is represented as an average instead of a tabulated count	64	59	0	0.09	0.06	1.03	0.70	0.48	0.33	0.44	0.67	1.37	0.10
DH20	See DH17-19, where the upper threshold is defined as the 25th percentile of median flows	64	62	1	0.01	0.04	0.15	0.48	0.08	0.26	0.70	0.74	0.14	0.12
DH21	See DH17-19, where the upper threshold is defined as the 75th percentile of median flows	64	61	1	-0.02	-0.05	0.28	0.77	0.14	0.38	0.45	0.62	0.21	0.16
DH22	Mean annual median interval in days between floods overall years	64	63	0	0.27	0.03	9.96	1.14	4.58	0.52	0.02	0.48	7.76	0.19
DH23	Mean annual number of days that flows remain above the flood threshold averaged across all years	64	39	1	0.01	0.08	0.06	0.74	0.03	0.40	0.39	0.60	0.06	0.14
DH24	Mean annual maximum number of 365 days over all water years during which no floods occurred over all years	64	64	1	-0.02	-0.09	0.15	0.87	0.08	0.47	0.22	0.53	0.13	0.16
TA1	Constancy	64	33	0	0.00	0.02	0.08	0.37	0.04	0.19	0.82	0.81	0.07	0.14
TA2	Predictability of flow	64	64	0	-0.09	-0.01	7.77	0.44	3.80	0.22	0.79	0.78	6.27	0.13
TA3	Seasonal predictability of flooding	64	25	1	0.00	0.05	0.07	0.78	0.03	0.37	0.03	0.63	0.05	0.26
TL1	Julian date of annual minimum	64	64	1	0.00	-0.03	0.03	0.71	0.02	0.36	0.60	0.64	0.03	0.12
TL2	Variability in Julian date of annual minimum	64	63	0	0.52	0.07	5.79	0.76	2.69	0.35	0.28	0.65	5.84	0.16
TL3	Seasonal predictability of low flow	64	4	0	0.00	0.11	0.01	0.57	0.00	0.31	0.23	0.69	0.01	0.21
TL4	Seasonal predictability of non-low flow	64	5	0	0.00	0.05	0.01	0.81	0.00	0.42	0.56	0.58	0.01	0.16
TH1	Julian date of annual maximum	64	64	1	-0.03	-0.09	0.24	0.63	0.12	0.31	0.22	0.69	0.46	0.13
TH2	Variability in Julian date of annual maximum	64	62	0	-0.10	-0.02	5.54	0.82	2.78	0.41	0.16	0.59	4.78	0.17
TH3	Seasonal predictability of non-flooding	64	32	1	0.02	0.11	0.13	0.80	0.07	0.42	-0.04	0.58	0.10	0.26
RA1	Rise rate	64	64	1	-0.09	-0.06	0.52	0.38	0.28	0.20	0.82	0.80	0.49	0.10
RA2	Variability in rise rate	64	64	1	0.00	0.02	0.15	0.71	0.08	0.39	0.34	0.61	0.13	0.15
RA3	Fall rate	64	64	0	11.69	0.09	44.26	0.36	26.46	0.21	0.68	0.79	64.04	0.12
RA4	Variability in fall rate	64	64	0	-1.13	-0.01	92.60	0.88	47.73	0.45	0.24	0.55	68.41	0.18
RA5	No day rises	64	15	1	0.00	-0.02	0.02	0.80	0.01	0.42	0.63	0.58	0.02	0.11
RA6	Change of flow (increasing flow)	64	37	1	0.01	0.04	0.06	0.41	0.03	0.20	0.73	0.80	0.06	0.11
RA7	Change of flow (decreasing flow)	64	21	0	0.00	0.05	0.02	0.26	0.01	0.15	0.67	0.85	0.03	0.10
RA8	Reversals	64	63	1	0.00	-0.02	0.10	0.86	0.05	0.47	0.19	0.53	0.08	0.19
RA9	Variability in reversals	64	63	0	0.19	0.05	3.82	1.03	1.88	0.50	0.20	0.50	4.14	0.15

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