Modelling Ecological Flow Regime: An Example from the Tennessee and Cumberland River Basins

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Abstract

Predictive equations were developed for 19 ecologically relevant streamflow characteristics within five major groups of flow variables (magnitude, ratio, frequency, variability, and date) for use in the Tennessee and Cumberland River basins using stepbackward regression. Basin characteristics explain 50% or more of the variation for 12 of the 19 equations. Independent variables identified through stepbackward regression were statistically significant in 78 of 304 cases ($\alpha > 0.0001$) and represent four major groups: climate, physical landscape features, regional indicators, and land use. Of these groups, the regional and climate variables were the most influential for determining hydrologic response. Daily temperature range, geologic factor, and rock depth were major factors explaining the variability in 17, 15, and 13 equations, respectively. The equations and independent datasets were used to explore the broad relation between basin properties and streamflow and the implication of streamflow to the study of ecological flow requirements. Key results include a high degree of hydrologic variability among least disturbed Blue Ridge streams, similar hydrologic behaviour for watersheds with widely varying degrees of forest cover, and distinct hydrologic profiles for streams in different geographic regions. Published in 2011. This article is a US Government work and is in the public domain in the USA.

Introduction

Implicit in ecological flow research is a deceptively simple conceptual model: Landscape factors, including climate, land cover, soil properties, and physiography, drive hydrologic response (streamflow), which in turn helps determine ecological outcomes, notably the composition, diversity, and resilience of riverine and riparian ecosystems. Streamflow thus links the broader landscape to ecological conditions in and near the stream channel. Because a stream's hydrologic response can be altered directly though water withdrawal or stream-channel modification (impoundment, dredging, filling, realignment, etc.) or indirectly through basin-scale changes in climate, land cover, and other landscape factors, better understanding of the relations among landscape, flow, and ecological health is a critical scientific and management need. Early workers in the field focused on establishing threshold values for specific flow characteristics required to maintain a minimum acceptable level of ecological integrity (Westgate, 1958; Rantz, 1964; Hoppe and Finnel, 1970; Tenant, 1976). More recently, a series of widely cited papers has urged analysis of the ecological function of a broad range of flow characteristics (flow regime) operating across a similarly broad range of temporal and spatial scales (Poff *et al*., 1997, 2010; Arthington *et al*., 2006).

Researchers seeking to implement studies linking ecological function to hydrology encounter a number of conceptual and practical challenges revolving around the essential complexity of flow regime. Early use of the term 'regime' in relation to streams was explicitly concerned with channel form and sediment transport (Bryan, 1922; Blench, 1957; Langbein and Iseri, 1960). In ecological flow studies, flow (also streamflow or hydrologic) regime is used somewhat more narrowly to represent what Langbein and Iseri (1960) call a stream's 'habits with respect to velocity and volume', in other words, the characteristic patterns of flow variation at a point along a stream. Description of flow regime thus encompasses the full suite of streamflow statistics (flow characteristics) characterized by measures of water yield, timing and frequency of flows, and all other aspects of hydrologic response, integrated across time scales ranging from instantaneous to millennia. The US Geological Survey's (USGS) StreamStats program for estimating flow characteristics in 23 states solves more than 2000 individual equations (Ries, 2007; http://water.usgs.gov/osw/streamstats/ssonline.html), but few hydrologists would consider it comprehensive.

The questions of which flow characteristics should be considered and whether or how to combine them have been addressed in a variety of ways, including grouping flow characteristics into functional categories, such as the magnitude, frequency, duration, timing, and rate of change in flow (Poff and Ward, 1989; Walker *et al*., 1995; Richter *et al*., 1996; Poff *et al*., 1997); programs for calculating suites of flow characteristics as potential ecological drivers (Swanson, 2002; Henrikson *et al*., 2006); stream classifications based on flow characteristics and environmental variables (Rosgen, 1994; Puckridge *et al*., 1998; Kennen *et al*., 2007, 2010; Hoos and McMahon, 2009; Kennard *et al*., 2009; Henriksen and Heasley, 2010); and screening of flow characteristics for statistical independence and ecological relevance (Olden and Poff, 2003; Knight *et al*., 2008; Acreman *et al*., 2009; Gao *et al*., 2009). Despite such efforts, the unwieldy number of flow characteristics and the lack of a common framework for evaluating their relative importance or combining them into a single representation of flow regime has impeded the drawing of general conclusions from an expanding literature of ecological flow studies (Poff and Zimmerman, 2010).

A practical challenge to relating flow regime to stream ecology is the relative sparseness of streamflow data in spatial and temporal terms. As of 2009, the USGS operated about 7700 active stream gauges in the United States or about one stream gauge per 1200 km^2, of which fewer than half had periods of record exceeding 40 years in length (D. Stuart, USGS, written communication, 2010). Biological data are typically collected on a much finer spatial scale. For example, Kennen *et al*. (2010) analysed 856 invertebrate sites across a 21 000 km^2 study area (1 site per 2.45 km^2). Knight *et al*. (2008) examined temporal and spatial overlap between records from about 1100 fish sampling sites and roughly 300 stream gauges in the intensely monitored Tennessee River basin (area 106 200 km^2)—one fish site per 96.5 km^2 and one stream gauge per 354 km^2. Only 33 sites met criteria of temporal overlap and locations no further apart than 4.8 linear stream kilometres. In the absence of suitable hydrologic datasets for most sites of potential interest, a consensus has emerged that hydrologic models are a crucial tool for quantifying interactions between streamflow and aquatic biota (Poff *et al*., 2010).

Hydrologic models can take a number of forms. An analytical framework proposed by Poff *et al*. (2010) emphasizes the simulation of daily streamflow hydrographs through numerical runoff models at the watershed scale. Part of the appeal of synthetic hydrographs lies in the flexibility they could provide. If a given suite of flow characteristics fails to explain ecological variation, a new suite might be derived from the simulated record. Watershed modelling has seen substantial improvements in recent decades (Singh and Woolhiser, 2002), and simulated hydrographs from regionally calibrated watershed models have been used to relate streamflow characteristics to invertebrate diversity and richness (Kennan *et al*., 2010).

Nonetheless, watershed model parameter estimation remains problematic. Problems with the reproducibility in *a priori* parameter estimation indicate that more improvement is needed before synthetic hydrographs can be generated with confidence for many ungauged basins across large regions (Hogue *et al*., 2004; Duan *et al*., 2006; Schaake *et al*., 2006). Moreover, modellers must choose from an array of alternative approaches to evaluate model error, where basin-scale calibration data are unavailable, none of which are generally accepted as definitive (Beven, 2006; Duan *et al*., 2006).

An alternative modelling approach is the statistical prediction of streamflow characteristics based on spatially distributed basin attributes. Regional statistical models have for decades been the standard approach for general purpose estimation of the magnitude, frequency, and duration components of flow regime (Benson, 1962a,b, 1964; Riggs, 1973; Tasker, 1982; Tasker and Stedinger, 1989; Tasker and Slade, 1994; Tasker *et al*., 1996; Law and Tasker, 2003; Ries, 2007; Law *et al*., 2009). The basic modelling approach, using multivariate linear regression could equally be applied to flow characteristics selected for ecological relevance. Statistical models lack the flexibility of simulated hydrographs for evaluating ecological flow requirements, but they offer benefits of quantifiable error limits and established diagnostic criteria (Helsel and Hirsch, 2002). Despite these advantages and widespread use in general hydrology, regional statistical models of flow characteristics have received only limited application in ecological flow studies (Sanborn and Bledsoe, 2006; Carlisle *et al*., 2009).

The application of hydrological models of any type to questions of ecological flows is in its early stages. General conclusions about which models are best suited to address which specific ecological questions will require a much larger pool of modelling studies across a range of spatial scales, regional contexts, and ecological questions.

This paper presents regional statistical models for 19 streamflow characteristics for free-flowing streams in the Cumberland and Tennessee River basins. Exploratory statistical and conceptual analysis on limited data have identified most (17 of 19) of these characteristics as having presumptive ecological relevance (Knight *et al*., 2008). A broader examination of the relations between streamflow and aquatic communities requires the ability to characterize flow regime where biological data are available but hydrologic data may not be. The models presented here thus represent an intermediate step towards such an examination. Further, we use these models to explore (1) the dependence of streamflow characteristics on specific basin attributes, (2) the potential effects of changes to those attributes on watershed hydrology, and (3) the integration of multiple streamflow characteristics into profiles that begin to statistically describe ecologically relevant aspects of flow regime for reference conditions at the regional scale. Although the models are developed specifically for the Tennessee and Cumberland River basins, the intent is to produce models that can be adapted for other locations.

Study Area

The predictive equations presented in this paper apply to sites across the Tennessee and Cumberland River watersheds, which drain approximately 106 200 and 46 830 km^2, respectively, and more than 150 000 km^2 combined. The Cumberland and Tennessee Rivers are adjacent tributaries of the Ohio River, which they join near Paducah, KY (Figure 1). Both rivers are regulated along much of their main stems and major tributaries. Major and many secondary urban centres are located along the main stems, most notably Nashville and Clarksville, TN, on the Cumberland River and Knoxville and Chattanooga, TN, Huntsville, AL, and Paducah, KY on the Tennessee River. Dominant nonurban land cover is forest, generally accounting for 50% or more of the total area, with pasture accounting for most of the remainder (Hampson *et al*., 2000; Woodside *et al*., 2004).

The Tennessee and Cumberland River basins represent a cross section of the area between the Appalachian divide and the Eastern Gulf Coastal Plain, including parts of five of

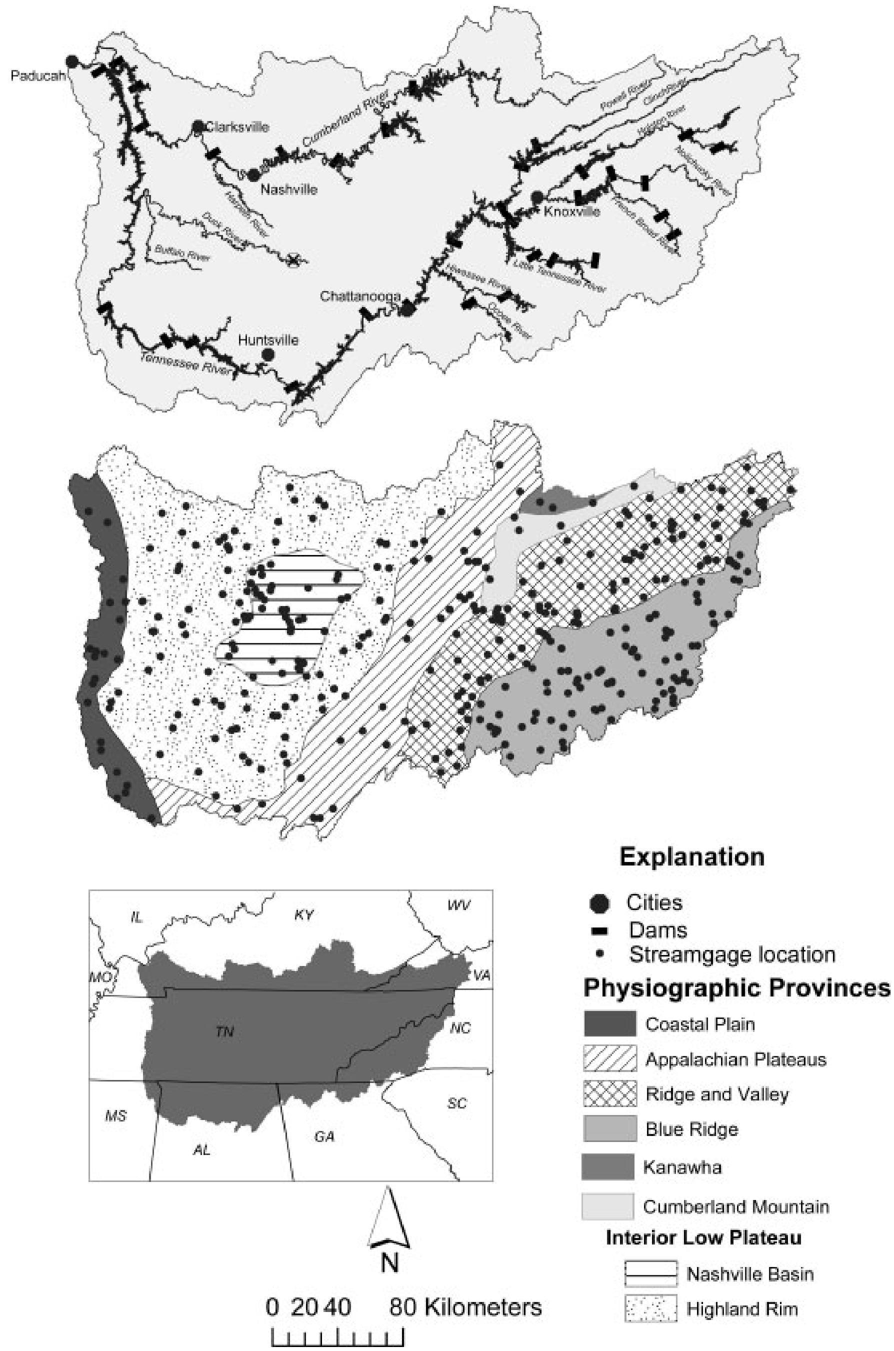

Figure 1. Tennessee and Cumberland River watersheds with physiographic provinces, dams, and major urban centres.

Fenneman's (1938) physiographic provinces, listed east to west: Blue Ridge, Ridge and Valley, Appalachian (Cumberland) Plateau (including Kanawha), Interior Low Plateau, and Coastal Plain. The Interior Low Plateau is further subdivided into the Highland Rim and Nashville Basin physiographic sections (Figure 1). Topographic slope, regolith thickness, and karst development vary substantially across the study area, producing regional variations in hydrologic response (Hoos, 1990; Wolfe *et al*., 1997; Law *et al*., 2009).

Temperature and precipitation in the study area vary with longitude and elevation. Average annual temperature in the area is 13.9 °C, while average annual temperatures across the area range from 11.1 °C in the northern Blue Ridge to 14.4 °C in the Interior Plateau. The warmest months of the year are July and August, and the coldest are typically January and February (US Department of Commerce, 2007a). The Interior Plateau averages about 1400 mm of precipitation annually, compared with 1350 mm in the Blue Ridge and about 1450 mm in the Cumberland Plateau and Ridge and Valley (US Department of Commerce, 2007b). Locally, precipitation in the Blue Ridge can exceed 2000 mm annually at the highest elevations.

Abell *et al*. (2000, p. 212) regard the Tennessee and Cumberland River basins as a single aquatic ecoregion, which they describe as 'contain(ing) the highest level of freshwater diversity in North America and (being) possibly the most diverse temperate freshwater ecoregion in the world' (Starnes and Etnier, 1986; Olsen and Dinerstein, 1998). This diversity includes 'an extraordinary 231 (fish species), of which 67 (29%) are endemic. . . a globally outstanding unionid mussel and crayfish fauna. . . are home to numerous species (of salamanders), many of which are restricted to the Tennessee-Cumberland' (Abell *et al*. 2000, pp. 212–213).

A wide range of human activities threaten these populations. Urbanization, mining, logging, agriculture, and other forms of land disturbance alter hydrologic response and contribute varying amounts of sediment, acids, bacteria, metals, and organic compounds to the area's rivers (Abell *et al*., 2000). Channelization and impoundments are pervasive throughout the Tennessee and Cumberland River basins. The resulting flow alteration has degraded or destroyed habitat and commonly accelerates channel erosion or sedimentation (Abell *et al*., 2000). Master *et al*. (1998, cited in Abell *et al*., 2000, p. 213) identified more than 57 fish species and 47 mussel species as being at risk in the Tennessee–Cumberland aquatic ecoregion. Aquatic invertebrates, such as the endemic Nashville crayfish (Orconectes shoupi), face similar threats (Clancy, 1997).

Analytical Approach

Multivariate statistical models were developed for each of 19 streamflow characteristics. Taken together, these models provide a profile of stream behaviour intended as an approximation of flow regime. Further analysis of the effects of flow regime on aquatic ecology requires models that are both predictive (can be applied to many ungauged locations) and meaningful (allow a comparison between streamflow characteristics and basin attributes). The extent to which constituent models serve both purposes depends on the structure of the models and the choice of independent variables, balancing parsimony and bias in the coefficients (Whittingham *et al*., 2006). To achieve a single coherent model of flow regime, the structure of the 19 constituent models was constrained in two important ways. First, all models were forced to share a common and limited pool of independent variables. Second, model inputs were standardized to allow direct comparison and summary of coefficients across models. To avoid overfitting, the independent variables considered for the final model included only those terms that were significant across multiple models. Given the large number of independent variable observations relative to the number of dependent variables (average >20 : 1) and error-degrees of freedom (219–223), no subsequent model validation was completed.

Dependent Variables

Daily mean streamflow data for stream gauges in the Tennessee and Cumberland River watersheds were downloaded from the USGS's National Water Information System (NWIS) database through NWISWeb (http://waterdata.usgs.gov/nwis/sw) and assembled into a database compatible for use with the hydrologic integrity tool (HIT) (Henriksen *et al*., 2006). All sites used in the analysis had a stream gauge with at least 10 years of daily mean streamflow data and had been screened for regulatory controls, such as hydroelectric dams (Law *et al*., 2009; Falcone *et al*., 2010). Sites with upstream control structures (such as hydroelectric and flood control) in the watershed were removed from the dataset due to the large hydrologic alteration imposed by such activities. Sites considered in the analysis do represent a range of land use conditions, including those that are indicative of human alteration. The regression models presented here are intended to predict current conditions on free flowing rivers and are for use in examining the relation of hydrologic alteration and fish community structure resulting from different landscape conditions, including conditions of increased urbanization. HIT was used to calculate streamflow characteristics presented in the study by Knight *et al*. (2008; table 1), which were used as dependent variables in this analysis. These characteristics represent aspects of the streamflow record presumed to partly determine fish community structure. In addition to the 17 characteristics presented in the study by Knight *et al*. (2008), the 15th percentile of streamflow (exceeded 85% of the time, e-85) and the median September daily streamflow were calculated for use as dependent variables. Median September daily streamflow was determined as the median of all daily streamflow values in the month of September available for a site. The e-85 and median September daily streamflow are highly correlated in the

Table I. Definitions of hydrologic metrics predicted using regression analysis.

	Hydrologic metric	Definition (units)
Magnitude	MA41—mean annual runoff	Compute the annual mean daily streamow and divide by the drainage area [cubic feet per second (cfs) per square mile (cfsm)]
	AMH10—maximum October streamflow	Maximum October streamow across the period of record divided by watershed area (cfsm)
	e-85—streamflow value exceeded 85% of time	85% exceedance of daily mean streamflow for the period of record normalized by the watershed area (cfsm)
	Sept_med—median September daily streamflow	Calculate the median of daily mean streamflow values for the period of record that occurred in the month of September normalized by watershed area (cfsm)
	LRA7—rate of streamflow recession	Log transform of the median change in log of flow for days in which the change is negative across the entire flow record (flow units per day)
Ratio	LDH13—average 30-day maximum	Log transform of the average over the period of record of the annual maximum of 30-day moving average flows divided by the median for the entire record (dimensionless)
	ML20—base flow	Divide the daily flow record into 5-day blocks. Assign the minimum flow for the block as a base flow for that block if 90% of that minimum flow is less than the minimum flows for the blocks on either side. Otherwise, set it to zero. Fill in the zero values using linear interpolation. Compute the total flow for the entire record and the total base flow for the entire record. ML20 is the ratio of total flow to total base flow (dimensionless)
	TA1—constancy	Measures the stability of flow regimes by dividing daily ows into predetermined flow classes (dimensionless)
	RA5—number of day rises	Compute the number of days in which the flow is greater than the previous day divided by the total number of days in the flow record (dimensionless)
Frequency	FH6—frequency of moderate flooding (three times median annual flow)	Average number of high-flow events per year that are equal to or greater than three times the median annual flow for the period of record. (number per year)
	LFH7—frequency of moderate flooding (seven times median annual flow)	Log transform of the average number of high-flow events per year that are equal to or greater than seven times the median annual flow for the period of record (number per year)
Variability	MA26—variability of March streamflow	Compute the standard deviation for March stream flow and divide by the mean streamflow for March (%)
	LML18—variability in base flow	Log transform of the standa rddeviation of the ratios of 7-day moving average flows to mean annual flows for each year multiplied by 100 (%)
	LDL6—variability of annual minimum daily average streamflow	Log transform of the standard deviation for the minimum daily average streamflow. Multiply by 100 and divide by the mean streamflow for the period (%)
	LDH16—variability in high-pulse duration	Log transform of the standard deviation for the yearly average high-flow pulse durations (daily flow greater than the 75th percentile) (%)
	FL2—variability in low-pulse count	Coef cient of variation for the number of annual occurrences of daily flows less than the 25th percentile (dimensionless)
Date	TL1—annual minimum flow	Julian date of annual minimum flow occurrence (Julian day)
	TH1—annual maximum flow	Julian date of annual maximum flow occurrence (Julian day)
	RA8—ow direction reversals	Average number of days per year when flow changes from rising to falling (or from falling to rising) (number per year)

Table adapted and modified from Knight *et al*., (2008).

streamflow dataset, with almost perfect one-to-one agreement. The e-85 and median September daily streamflow represent flow levels in the annual hydrograph that are critical to aquatic biota (Annear *et al*., 2004) and commonly referred to in regulations or policy statements related to ecological flow requirements (Tennessee Wildlife Resources Agency, 2010). The final dependent-variable dataset consisted of 19 streamflow characteristics (Table I) for each of 231 sites in the Tennessee and Cumberland River basins. All dependent data were standardized to a mean of zero and a standard deviation of one prior to analysis. Dependent data were grouped according to the aspect of the flow regime they describe: magnitude, ratio, frequency, variability, and date (M, R, F, V, and D, respectively; Table I).

Independent Variables

Selection of independent variables was driven by the spatially and temporally varied nature of the streamflow characteristics being predicted. Initial basin characteristics considered for use in the development of predictive equations were compiled using two resources. Prior regression analyses by Law and Tasker (2003) and Law *et al*. (2009) provided several basin characteristics for sites in the Tennessee and Cumberland River watersheds including drainage area, main-channel slope, mean basin elevation, soil factor, and geologic factor. Drainage area was used to normalize magnitude variables and was not considered as an independent variable. Additional characteristics were derived using geographic information system (GIS) basin-weighting techniques based on the following geospatial data layers: climate (Daly *et al*., 2008), 2001 National Land Cover (Homer *et al*., 2004), flow processes (Wolock, 2003a,b), soil indices (Wolock, 1997; Greene and Wolfe, 1998), climate data (Daly *et al*., 2008), and depth to bedrock (Wolock, 1997). Continuous, digitally gridded climate data were downloaded from Parameter-elevation Regressions on Independent Slopes Model (Daly *et al*., 2008) and represent maximum, minimum, and average temperature and average precipitation for annual and monthly time periods based on the 1971–2000 means. A dataset of more than 30 potential independent variables that represented functional/flow governing processes was compiled from previous work (Law and Tasker, 2003; Law *et al*., 2009) and GIS analysis. All independent data were standardized to a mean of zero and a standard deviation of one prior to analysis.

Variable Screening and Reduction

A combination of bivariate plots, parametric correlation analysis, and principal component analysis were used to identify independent variables that were most meaningful for prediction, were least redundant, and minimized overspecification. Visual patterns of bivariate association were used to identify and remove highly correlated variables. Spearman rank correlation values (ρ), using the dependent and independent dataset, greater than or equal to 0.6 were used as a second screening criterion to remove or combine independent variables and identify a subset of variables useful in predicting streamflow characteristics with minimal covariance. This subset of standardized independent variables was then checked for within-group correlation. A screening criterion of greater than or equal to 0.8 within independent variables was used to remove highly correlated independent variables. In general, the variables that were most readily available and contained the most predictive information were kept. Principal components analysis yielded similar results for between and within-group analysis.

Further variable reduction was accomplished by removing one variable from groups of variables that sum to a constant. Such groups produce a singularity in the solution matrix, confounding determination of a unique 'best' solution (Marcoulides and Hershberger, 1997). We reduced this effect by removing the most highly correlated variable from the affected variable group. For example, we removed 'percent developed' from consideration because the sum of all land use percentages always equals 100. Elimination of overspecification avoids singularity while preserving the original information in the model.

The final set of 16 independent variables represent physical determinants of how much water is available to the system, how that water is stored, delivered to streams, and subsequently transported. Thirteen of these variables can be grouped into four functional categories: climate, land use, physical properties, and regional variables. Some of these categories, such as the region from which a stream is flowing or the physical properties of soil thickness, may be relatively fixed and independent of human alteration. Other categories, such as climate and land use, may be subject to considerable change. The relative contributions of these categories, reflected by their importance in the predictive equations, may indicate their susceptibility to alteration through environmental change.

Interactions among independent variables were evaluated by multiplying terms. Initial exploration using correlation analysis as well as preliminary model runs indicated that significant interactions were limited to combinations of 'mean monthly precipitation' with three other variables—'soil factor, rock depth, and geologic factor'. The products of these terms are suggestive of the volume of water held in the regolith and underlying aquifers available for baseflow. Resulting interaction terms were included in the independent variable dataset (Table II).

Statistical Methods

Multivariate regression was used to develop statistical models relating basin properties to streamflow characteristics throughout the study area. Variables were removed from the model when individual statistical significance (*p* value) was 0.2 or greater. The stepbackward (stepwise backward elimination) technique was chosen to minimize the number of terms in a model without overly biasing the remaining terms. Using a *p* value of 0.2 provided a similar result to single-step elimination of all nonsignificant terms (Whittingham *et al*., 2006). Model output was derived using standardized (mean of 0 and a standard deviation of 1) basin properties (independents) and streamflow characteristics (dependents). Models are in the basic form of a linear multivariate Equation (1).

$$Y = \beta_0 X_0 + \beta_1 X_1 + \ldots + \beta_n X_n \tag{1}$$

where Y is the dependent variable of interest, and β_i and X_i are model coefficient and value of the ith independent variable, respectively. Standardization consisted of subtracting the mean of each independent variable (Table III) from that variable's value and then dividing that quantity by the variable's standard deviation (Equation (2)). Equation results can be converted back to nonstandardized form by multiplying each predicted value by the corresponding observed standard deviation and adding the observed mean (Table III) (Equation (3)).

$$X' = (X - \overline{X}) / \mathrm{SD} \tag{2}$$

$$Y = Y' \times \mathrm{SD} + \overline{Y} \tag{3}$$

where X is the independent variable, X' the standardized form of the independent variable, $\overline{X}$ the mean of the independent variable, Y the dependent variable, Y' the standardized form of the dependent variable, $\overline{Y}$ the mean of the dependent variable, and SD is the standard deviation.

Regression coefficients determined from standardized data were used to compare the importance of independent variables. These are commonly referred to as beta-weights in which magnitudes express the relative influence (weight) of each independent term on model predictions (Landis, 2005). Newman and Browner (1991) discuss the relative usefulness of beta-weights at comparing associations between predictor variables (independents) and outcomes within and between populations. The absolute value of beta-weights computed for similarly structured constituent models of streamflow characteristics were summed across multiple models to provide a general indication of the relative importance of watershed attributes on overall flow regime. Although beta-weights may be misinterpreted in the presence of strong covariance (Greenland *et al*., 1986, 1991), the approach has value in comparing multiple models (Criqui, 1991) when care is taken to minimize covariance.

Table II. Definitions for independent variables used in predictive equations.

Variable	Definition
Climate	
Monthly mean precipitation	Average annual precipitation divided by 12 (mm) (Daly *et al*., 2008)
Jan precipitation deviation	Mean January precipitation divided by monthly precipitation mean (mm) (Daly *et al*., 2008)
Daily temperature range	Mean maximum daily temperature minus mean minimum daily temperature (°C) (Daly *et al*., 2008)
August temperature deviation	Mean August maximum temperature minus mean annual temperature divided by mean annual temperature (°C) (Daly *et al*., 2008)
Land use	
Forest	Percent forest cover—the total percentage of land cover in a watershed that is considered to be forested (%) (Homer *et al*., 2004)
Agriculture	Percent agricultural cover—the total percentage of land cover in a watershed that is considered to be agricultural (%) (Homer *et al*., 2004)
Physical	
Horton	Index of Hortonian overland (infiltration excess) (dimensionless) (Wolock, 2003a, b)
Mean elevation	Mean basin elevation derived from 1/3 arc-second digital elevation model (feet) (Gesch *et al*., 2002; Gesch, 2007)
Soil factor	Percentage of area underlain by soil with a permeability of at least 5 cm $\cdot h^{-1}$(percentage) (Greene and Wolfe, 1998)
Rock depth	Average depth of soil above bedrock (feet) (Wolock, 1997)
Regional	
Geologic factor	Measure of the number of days that pass as discharge recedes one complete log cycle of streamflow (days) (Bingham, 1986)
Blue Ridge	Percent of the watershed that lies within the Blue Ridge level 3 ecoregion (calculated from Omernik, 1987)
Interior Plateau	Percent of the watershed that lies within the Interior Plateau level 3 ecoregion (calculated from Omernik, 1987)
Interaction Terms	
Soil factor	Soil factor multiplied by monthly mean precipitation
Rock depth	Rock depth multiplied by monthly mean precipitation
Geologic factor	Geologic factor multiplied by monthly mean precipitation

All variables represent average values for a basin with the exception of Blue Ridge, Interior Plateau, forest, and agriculture, which are expressed as the percent of total watershed area.

[Correction added after online publication 22 December 2011: the definition of 'August temperature deviation' has been changed]

Results

Model Coefficients

Final models retained as few as 6 and as many as 12 independent variables significant in predicting streamflow characteristics. 'Daily temperature range' was the most common, appearing in 17 equations, while the interaction term 'soil factor—monthly mean precipitation' was least often used (three times) (Table III). 'Geologic factor' had the greatest total weight (a sum of the absolute values of 4.9398 across all equations), may have the greatest influence overall, and was significant in 14 models. This variable was closely followed by 'mean elevation', with an aggregate beta weight of 4.4012 across 11 models. The interaction term 'soil factor—monthly mean precipitation'—was the least powerful term (aggregate weight 0.7415). Streamflow characteristics describing magnitudes (M) are overwhelmingly influenced by variations in 'monthly mean precipitation' (2.057), 'geologic factor' (1.190), and 'percent Interior Plateau' (0.9382). Streamflow characteristics describing frequencies (F) are strongly influenced by 'mean elevation' (0.8520), 'percent of agricultural land use' (0.6836), 'percent Interior Plateau' (0.4453), and geologic factor (0.4377). Streamflow characteristics for ratio (R) and variability (V) measures appear to be most strongly related to 'geologic factor' (1.046 and 2.129, respectively). 'Percent Blue Ridge' (0.7809) and 'mean elevation' (0.6936) represent a second tier of influence for ratio characteristics, while 'mean elevation' (1.2863) and 'percent Interior Plateau' (1.1847) represent second tier influence for variability characteristics. 'Mean elevation' (0.9296), 'percent Blue Ridge' (0.5688), and 'August temperature deviation' (0.5575) provide the most explanatory power for streamflow characteristics of the date (D) group. The frequency (F) and variability (V) groups have higher total beta weights per number of predictive models within the respective groups (2.59 and 2.22, respectively).

While all variable categories were significant in all predictive equations, the regional variables appear to have the greatest importance based on aggregate beta weights summed across all equations, followed by climate, physical, and finally land use variables. Regional variables were used in 17 of 19 equations. 'Geologic factor' had the highest incidence of statistical significance (12 equations). Six of the seven most predictive models (LDH13, E85, ML20, LFH7, Sep_med, and MA26) used all three regional variables. Climate variable beta weights were among the highest, reflecting the intimate relation between climatic and hydrologic variability. 'Daily temperature range' was used in all but two models (LDL6 and RA8). All climate variables were used in two magnitude equations (e85 and Sep_med). Variables in the physical category were used in all 19 equations. 'Mean elevation' and 'Horton' (Hortonian overland flow coefficient, Table II) were the most commonly used physical variables, being used in 12 equations, while mean elevation was significant in 5 equations. 'Soil factor' and 'rock depth' were significant in four and three equations respectively, appearing in nine and ten equations, respectively (Table III). Land use played a major

Table III. Variable coefficients for independent variables for predicted hydrologic metrics.

Dependent variable	MA41	LRA7	E85	SEP_Med	AMH10	LDH13	ML20	TA1	RA5	LFH7	FH6	LML18	LDL6	MA26	LDH16	FL2	TL1	TH1	RA8	Total Beta weight	Mean	Sdev
Regime	M	M	M	M	M	R	R	R	R	F	F	V	V	V	V	V	D	D	D		(of original data)	
Climate																						
Monthly mean precipitation	0·8289	−0·1106	0·3827	0·3999	0·3350	−0·1117	—	—	−0·3039	—	—	0·1969	0·2160	—	0·2158		—	−0·2985	—	3·3998	119·9839	14·6415
Jan precipitation deviation	—	—	0·0684	−0·1091		0·0944	0·0579	0·0891	—	—	—	−0·1655	−0·3368	—	—	−0·1580	0·3013	—	—	1·3806	1·0760	0·0899
Daily temperature range	−0·1371	−0·1476	0·0952	0·0670	−0·2519	−0·1403	0·1622	0·2012	0·1183	−0·1849	−0·1609	−0·1053	—	−0·0631	0·1069	0·2478	0·2107	0·2878	—	2·6882	12·7968	0·6179
Aug Temperature deviation	0·1563	—	0·1236	0·1065	—	—	—	0·1981	—	0·1135	0·2197	−0·3285	−0·4313	—	—	−0·2808	—	−0·3514	0·2061	2·5158	1·2291	0·1222
Land use																						
Forest	—	—	−0·0876	−0·0930	−0·1978	0·1474	—	0·1812	—	—	−0·3242	—	—	0·1958	—	0·2568	−0·1789	—	—	1·6628	63·0991	21·9919
Agriculture	—	−0·2211	—	—	−0·2802	—	0·2189	0·2929	—	−0·1604	−0·5232	—	−0·1036	—	0·1664	0·4934	0·3373	—	0·1143	2·9117	27·0930	19·0429
Physical																						
Horton	0·0462	—	—	—	0·3738	0·0600	−0·0914	−0·1047	−0·1425	0·1063	0·2098	—	—	0·1124	—	—	—	−0·2141	—	1·4611	4·5305	2·1091
Mean elevation	0·1383	—	—	—	0·4987	−0·2095	0·1509	—	0·3359	−0·3251	−0·5269	0·3458	0·4420	−0·2607	−0·2379	—	0·9296	—	—	4·4012	1772·2752	1048·1326
Soil factor	—	−0·1407	—	—	—	−0·1735	0·1078	0·1269	—	−0·0932	−0·1669	—	−0·2209	−0·2575	0·2193	—	0·2514	—	—	1·7580	56·7143	20·8192
Rock depth	−0·0408	−0·1369	0·1457	0·1445	−0·1027	—	0·1285	—	−0·0958	−0·1263	−0·1541	−0·1671	—	—	—	0·3158	−0·2604	—	−0·1615	1·9801	1·2154	0·2171
Regional																						
Geologic factor	—	−0·5825	0·3138	0·2936	—	−0·2965	0·4267	0·3233	—	−0·2644	−0·1733	−0·6103	−0·6308	−0·2657	0·3268	0·2949	—	−0·1372	—	4·9398	95·6190	50·7355
Blue Ridge	—	—	0·2957	0·3156	—	−0·3230	0·2194	0·2385	—	−0·3167	—	—	—	−0·1210	0·2740	—	−0·4095	—	−0·1593	2·6728	31·3356	45·3390
Interior Plateau	—	0·3207	−0·2290	−0·2534	0·1351	0·3056	−0·3111	—	—	0·2605	0·1848	0·2530	—	0·3318	—	−0·6000	—	—	0·3007	3·4856	34·8059	46·6213

Table III. (*Continued*).

Dependent variable	MA41	LRA7	E85	SEP_Med	AMH10	LDH13	ML20	TA1	RA5	LFH7	FH6	LML18	LDL6	MA26	LDH16	FL2	TL1	TH1	RA8	Total Beta weight	Mean	Sdev
Regime	M	M	M	M	M	R	R	R	R	F	F	V	V	V	V	V	D	D	D		(of original data)	
Interaction (multiplied by monthly precipitation mean)																						
Soil factor	0·1189	—	0·0540	0·0839	0·3056	—	—	—	—	—	—	—	—	—	—	—	—	−0·1791	—	0·7415	—	—
Rock depth	—	0·1924	—	—	—	0·1182	−0·1583	—	0·1171	0·1518	0·2750	0·1184	0·1081	0·2149	—	—	−0·1614	—	0·1094	1·7250	—	—
Geologic factor	0·0912	−0·0733	0·1479	0·1448	0·1726	—	0·0756	—	—	−0·0759	−0·0793	−0·1020	−0·1094	−0·0782	—	—	—	—	—	1·1502	—	—
Total beta weight	1·5578	1·9256	1·9437	2·0113	2·6534	1·9802	2·1087	1·7560	1·1134	2·1790	2·9980	2·3927	2·5989	1·9011	1·5472	2·6474	3·0404	1·4681	1·0513	—	—	—
Mean (of original set)	1·8062	−0·9539	0·3550	0·3946	3·5988	0·8350	0·4474	0·4463	0·2586	0·7915	12·1129	1·6571	1·6366	85·2389	1·5770	46·1098	265·4498	43·3120	10·1448	—	—	—
Sdev (of original set)	0·5178	0·1581	0·3259	0·3782	2·8643	0·2491	0·1448	0·1473	0·0322	0·3203	3·2938	0·2456	0·2564	30·0974	0·1544	8·9174	12·3660	21·0262	3·3595	—	—	—
Number of parameters in model	8	9	11	11	10	11	12	9	6	12	12	10	9	10	7	8	9	6	6	—	—	—
Error degrees of freedom	223	222	220	220	221	220	219	222	225	219	219	221	222	221	224	223	222	225	225	—	—	—
r^2	0·9107	0·6689	0·8990	0·8928	0·6364	0·8453	0·8362	0·5225	0·2700	0·8588	0·5872	0·5185	0·4734	0·7201	0·3693	0·3846	0·4228	0·2405	0·1505	—	—	—
RMSE	0·3058	0·5890	0·3263	0·3365	0·6205	0·4049	0·4164	0·7083	0·8720	0·3877	0·6603	0·7117	0·7447	0·5449	0·8140	0·8018	0·7822	0·8850	0·9415	—	—	—

Coefficients are beta weights derived from standardized independent variable values in and can be used to infer meaning/strength of relationship between a given independent and the dependent.
Shaded coefficients represent values that were significant at the $p < 0.001$ level; gray shading denotes different classes of metrics; total beta-weights are based on the absolute values of beta-weights.
—, Independent variable not used in model; M, magnitude; R, ratio; F, frequency; V, variability; D, date; sdev, standard deviation.

role in 15 of 19 equations and statistically significant in 7 equations. In five equations where both 'percent agriculture' and 'percent forest' were present, beta-weights indicated that 'percent agriculture' was between 1.5 and 2 times as important compared with 'percent forest' (based on beta-weights) were of about equal importance. Beta-weights also suggest that land use variables are most important in determining frequency of moderate flooding (FH6) and variability in low pulse count (FL2). Maximum October runoff and frequency of moderate flooding were inversely related to the 'percent forest' and 'percent agriculture', while constancy and variability in low pulse count were positively correlated to the 'percent forest' and 'percent agriculture'. While land use variables were influential in 15 predictive equations, they were ranked fourth of the four independent variable groups when considering overall average aggregate beta-weight per time used in an equation.

Fit Statistics

High-aggregate beta-weight across all terms in a given model generally corresponds to higher r^2 values for predictive equations and generally increases with increasing number of model parameters (Table III; Figure 2). This was also true when considering the dependent-variable groups (magnitude, frequency, ratio, variability, and date). The average number of model parameters and r^2 values for the magnitude (9.8, 0.8016) and frequency (12, 0.7230) groups were higher than for the ratio (9.5, 0.6185), variability (8.8, 0.4932), and date (7, 0.2713) groups. The five highest r^2 values (MA41, LDH13, E85, ML20, and LFH7) varied by less than 0.065 (Table III). The r^2 values decline more steeply below the top five, down to 0.27, 0.24, and 0.15 for the lowest three models. Poor model fit suggests that significant determinants of a particular streamflow characteristic were not adequately represented in the independent variable set. The top five models used an average of 10.6 independent variables (66% of the available independent variables) compared with the remaining 14 models, which used an average of 8.78 independent variables (55% of available independent variables) (Table III).

Streamflow characteristics in the magnitude and frequency groups have lower average root mean square error (RMSE) values (0.4356 and 0.5240, respectively) compared with ratio (0.6004), variability (0.7234), and date groups (0.8695) (Table III). RMSE values indicate the share of the dependent variable standard error that remains unexplained in the model. RMSE varied from a high value of 0.9415 for the prediction of the number of flow reversals (RA8) to a low value of 0.3058 for the prediction of the mean annual runoff (MA41) (Table III). The RMSE for the number of flow reversals (RA8) indicates that only 5.85% (1–0.9415) of the original standard error was removed by the model. The RMSE for mean annual runoff indicates that 69% (1–0.3058) of the original standard error was removed by the model.

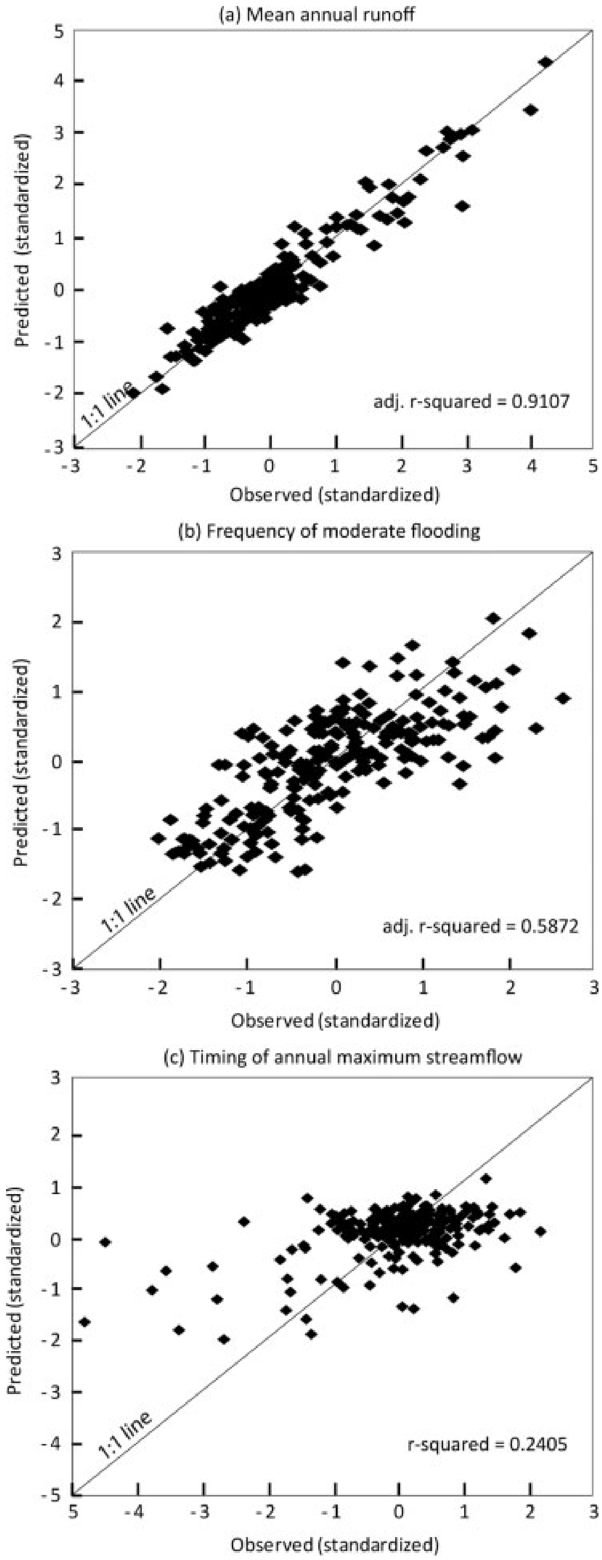

Figure 2. Comparison of standardized values of observed and predicted values across range of model fits for (a) mean annual runoff (MA41) (nine variables), (b) frequency of moderate flooding (FH6) (11 variables), and (c) timing of annual maximum streamflow (TH1) (6 variables).

Implications for Defining Ecological Flow Requirements and Limits of Hydrologic Alteration

Ecological flow studies have as their object, understanding and identifying the limits of hydrologic alteration based on ecological response to a quantifiable hydrologic change from some reference condition (regime) that is unique to streams in a given region (Poff *et al*., 1997, 2010). Implicit in this effort is a general conceptual model in which changes in basin conditions alter hydrologic response relative to some hydrologic reference condition, followed by consequential ecological change (Arthington *et al*., 2006). The following discussion is a preliminary examination of the broad relation between basin properties and streamflow and its implications for the study of ecological flow requirements. We begin that examination with a few key questions:

1. Which streamflow characteristics, at what levels of precision and accuracy, are appropriate to define a reference flow regime?

2. How large a departure from a specific reference condition can aquatic communities tolerate?

3. Can regional patterns in hydrologic alteration be associated with specific ecological community responses?

4. Which hydrologic characteristics are most useful in comparing sites and regions to reference conditions to quantify hydrologic alteration?

5. Which types of conceptual and mathematical models best address ecological effects of hydrologic alteration?

To begin addressing these questions, we consider the distributions of observed and predicted values for 19 modelled streamflow characteristics in the 20 least disturbed (>91% forest cover) basins in the Blue Ridge. The basins represent the least disturbed landscape condition in the Tennessee–Cumberland system, which is recognized for its globally significant aquatic biodiversity (Abell *et al*., 2000). Furthermore, most of these basins lie wholly or substantially on protected public lands. In the absence of detailed ecological data, these streams can be presumed to provide reference quality habitat and hydrologic conditions. The middle 50% (interquartile range) of values for these streamflow characteristics captures the space in which a reference flow regime for the Blue Ridge would likely reside. That baseline is graphically represented by ordering (arbitrarily) observed Blue Ridge median departures from the overall mean (mean of the standardized data, in this case zero) highest to lowest. Observed median departures range from nearly 1.9 (MA41) to about –1.2 (LDH13) standard deviations (Figure 3(a)).

Rather than considering any single stream as defining a unique hydrologic reference condition, it may be more useful to seek a general set of hydrologic conditions that delineate a

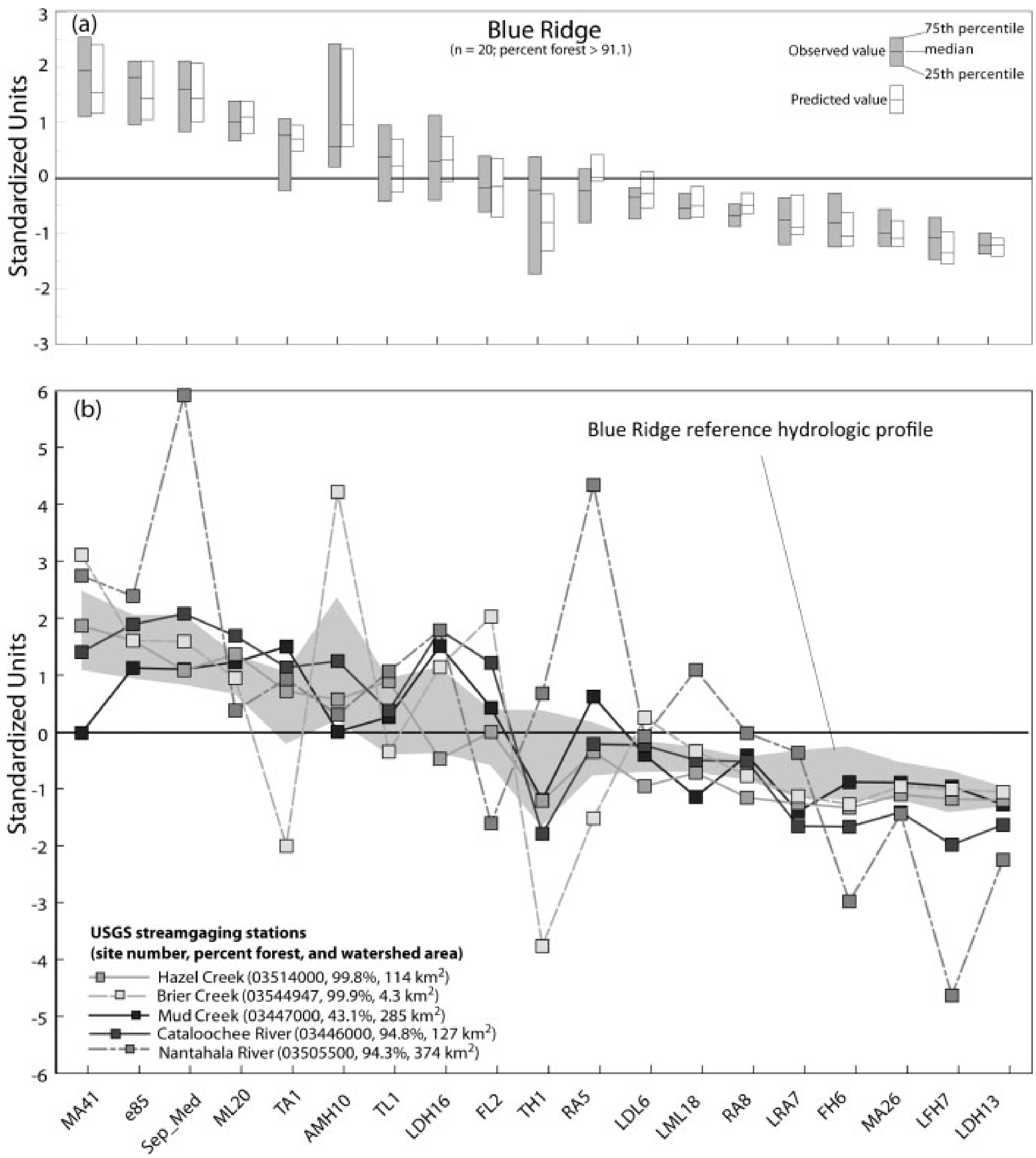

Figure 3. Precision and accuracy of predicting the Blue Ridge hydrologic response profile were assessed by comparing the interquartile range of the predicted and observed streamflow characteristics for minimally altered wateshesds in Blue Ridge physiographic province (a) and for selected USGS streamgaging stations (b) (http://waterdata.usgs.gov/nwis/sw).

reference 'hydrologic profile' for the Blue Ridge. Published discussion of hydrologic reference conditions related to stream ecology appears to consider the hydrologic variability of single streams, often referred to as 'natural hydrologic regimes' (Jacobson and Galat, 2008). However, each of the streams represented in Figure 3 occupies its own flow regime with inherent variability and unique descriptive hydrologic statistics; any of these individual flow regimes might plausibly be regarded as a 'reference', with little basis for preferring one over another. Collectively, the 20 sites plotted in Figure 3(a) (observed values) define a distinctive pattern characterized by (1) the signs and magnitudes of the median departure from the overall mean, (2) the ordering of such departures from largest to smallest, and (3) the overall and interquartile ranges of each characteristic. Such patterns may provide a reasonably robust and stable basis for inferring hydrologic reference conditions (*sensu* Arthington *et al*., 2006).

Working from the assumption that 20 watersheds in the Blue Ridge with more than 91% forest cover represent an undisturbed and presumably tolerable set of hydrologic conditions, the range of ecological tolerability might be inferred from the range of observed variability of ecologically relevant streamflow characteristics. The observed interquartile ranges for the 19 streamflow characteristics range from about 0.5–2 standard deviations on the standardized scale (Figure 3(a)), but the range of tolerability for organisms may be greater. The observed interquartile ranges define an empirical hydrologic profile, which approximates the central tendency of the reference hydrologic profile.

A plot of actual values for the 19 streamflow characteristics (Figure 3(b)) shows at least three distinct patterns of departure from the overall mean. The Cataloochee River and Hazel Creek plot close to the central tendency of the left-to-right descent of the 19 medians, while both Brier Creek and the Nantahala River (both flow controlled) show substantial departures (Figure 3(b)). The pattern of departure shown by Brier Creek is shared with varying, and generally smaller, magnitudes by several of the 20 least disturbed sites in the Blue Ridge. The pattern shown by the Nantahala River provides evidence of the usefulness that hydrologic response profiles in determining departures from a reference conditions. Although the Nantahala River is a nearly pristine watershed, flow from 60% of the basin is controlled by a reservoir.

A comparable plot of values for Mud Creek, the least forested (43%) watershed analysed in the Blue Ridge, lies close, with a few exceptions, to the central tendency traced by the plots for the Cataloochee River and Hazel Creek (Figure 3(b)). This result is somewhat unexpected given that land use was an important term in 15 of 19 equations. However, this also compliments the earlier finding that land use was the fourth of four independent variable groups in regard to average aggregate betaweight across all models. Nonetheless, this finding suggests that forest cover, while useful in predicting streamflow characteristics, does not fundamentally change the region of hydrologic response, at least across the range of forest cover (40–100%) considered for the Blue Ridge in this study. Significantly lower forest cover in the Mud Creek watershed fails to produce hydrologic departures approaching those displayed by the nearly pristine, yet controlled, Nantahala River and practically pristine Brier Creek (Figure 3(b)).

Regions of hydrologic response appear to be unique for each principal geographic region and do not appear to be related to differences in forest cover. Median and quartile departures from the overall mean for the same 19 streamflow characteristics in Ridge and Valley and Interior Plateau produce distinct regional patterns that contrast with that of the Blue Ridge when plotted in the same left-to-right order (Figure 4). Observed and predicted values are represented for the 20 least disturbed sites in the Ridge and Valley (>61% forest cover) and the Interior Plateau (>59%) (Figure 4). Compared with the Blue Ridge, both the Ridge and Valley and Interior Plateau show a clear reversal of slope in the region of hydrologic response. These two regions show lower overall flow magnitudes (left side of plot) and higher variability characteristics (right side of plot) than that seen in the Blue Ridge. There are notable differences between the Interior Plateau and Ridge and Valley, including lower interquartile ranges for most characteristics in the Ridge and Valley and lower median departures for extremes (AMH10 and LDH16) (Figure 4). The intermediate hydrologic character of the Ridge and Valley is consistent with previous analyses (Knight *et al*., 2008).

Streamflow characteristics that are furthest from the mean (standardized units = 0) have smallest interquartile ranges and can be predicted with the greatest accuracy, and precision may be the most useful for comparing sites, regions, and reference conditions. These are characteristics on the extreme left and right of Figures 3 and 4. In general, these characteristics also have the highest prediction coefficients (r^2 in Table III). Overall, the models perform well, predicting the central regional hydrologic profile across the range of characteristics. However, review of predicted characteristics for the Nantahala River and Brier Creek shows that they fall within the central regional hydrologic profile and do not display the strong departures seen with the observed characteristics. This provokes two observations. The first is that some stations display considerable hydrologic variation that is unaccounted for within the predictive models. The second is that the predictive models may reasonably be assumed to capture an intrinsic hydrologic behaviour that is broadly descriptive of the geographic region.

We have noted reservations about the feasibility of developing precise and accurate analytical watershed models across broad regions (Hogue *et al*., 2004; Duan *et al*., 2006; Schaake *et al*., 2006). Our analysis raises the question of whether such models, even if feasible, are well suited to the task of discriminating between ecologically tolerable and intolerable hydrologic conditions. The wide range of variability within the hydrologic response region defined by least disturbed basins in the Blue Ridge suggests that incremental hydrologic change need not have a discernible ecological effect. Moreover, the location of a relatively disturbed stream, such as Mud Creek, near the centre of the approximated regional hydrologic profile for the Blue Ridge suggests that regional hydrologic profiles may be able to absorb considerable land cover alteration without significant, or even discernible, hydrologic change.

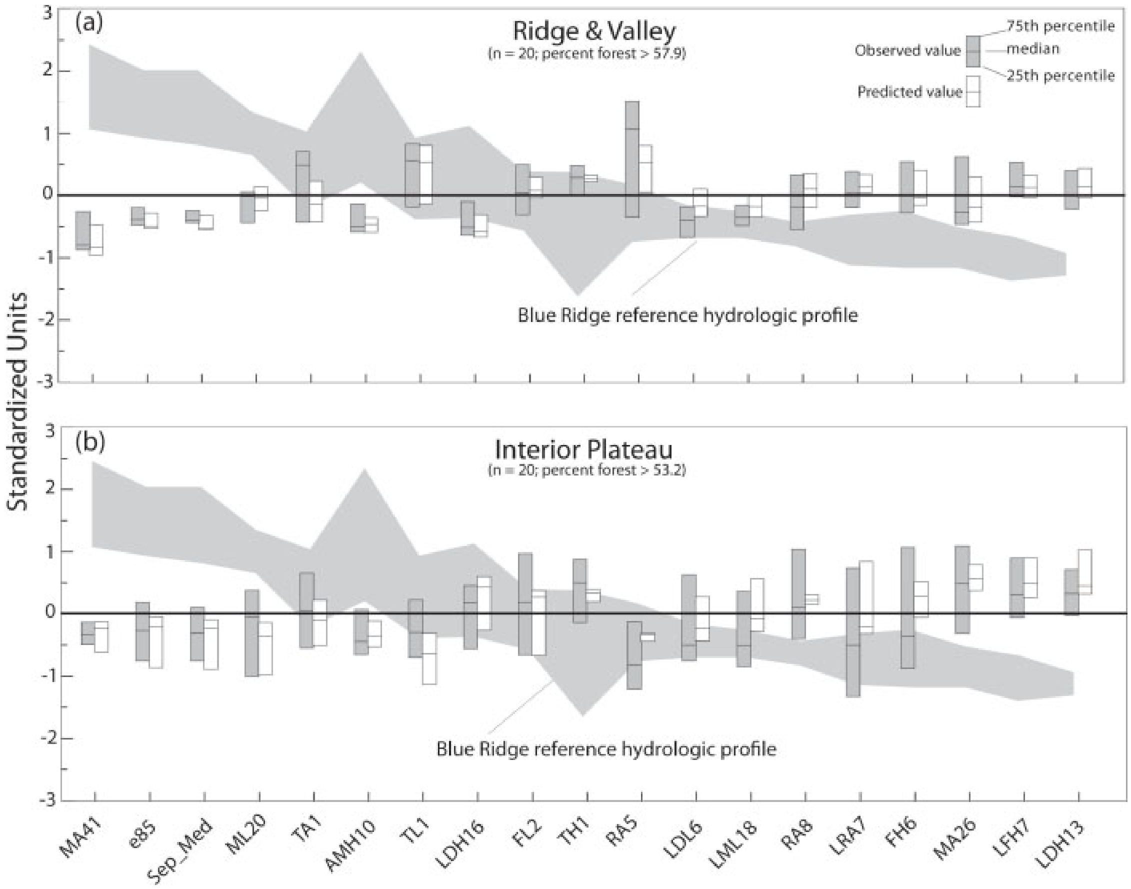

Figure 4. Interquartile ranges for observed and predicted values of 19 sttreamflow characteristics for 20 least disturbed watersheds in the Ridge and Valley (a) and Interior Plateau (b) physiographic regions compared with the observed central hydrologic response profile for the Blue Ridge.

Conclusions

This paper presents an approach to ecological streamflow requirements based on statistical modelling. This approach is innately suitable to hydrologic characterization at the regional scale and illuminates the influence of independent environmental factors on hydrologic response. Resulting analysis examines regional hydrology in a way that integrates an array of characteristics across multiple streams to delineate regional hydrologic profiles, which provide an analytical framework for classifying streams and examining the relation between ecological integrity and streamflow characteristics. Preliminary application of that framework in this paper suggests both hydrologic resilience in the face of landscape change and ecological resilience in the face of hydrologic change. The limits of such resilience remain an open question. Determining those limits will require an analysis of ecological data at a similar spatial scale including correlation with reliable estimates of streamflow characteristics. From this, it may be possible to determine where and under what conditions aquatic communities are limited by flow regime.

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