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Exploring the Consistency of Flow Regimes Within and Among Ecoregions of the Southeastern United States

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EXPLORING THE CONSISTENCY OF FLOW REGIMES WITHIN AND AMONG ECOREGIONS OF THE SOUTHEASTERN UNITED STATES

by

FRANK PAUL BRAUN IV

(Under the Direction of James H. Roberts)

ABSTRACT

Human manipulation of river systems has long been a known contributor to the loss of freshwater biodiversity. By accounting for environmental causes of hydrologic variation among rivers, we can better understand how ecoregion mediates flow regimes and forecast species that may be at risk. Presumably, natural variation associated with ecoregion boundaries exerts strong influence on flow regimes, and may mediate relationships between other features (e.g., land use, dams) and hydrology. However, such between-ecoregion variation is poorly investigated, particularly at fine spatial and temporal scales. I characterized 10 hydrologic metrics, representing the dimensions of the flow regime (magnitude, frequency, duration, timing, and rate-of-change) using 30+ years of streamflow data collected at 375 monitoring gages in streams spanning mountain (MT), Piedmont (PD), and coastal plain (CP) ecoregions of the southeastern U.S. Random forest and redundancy analysis models were used to rank the relative importance of stream-size, land-cover, climatic, physiographic, and impoundment conditions in upstream watersheds for predicting downstream flow characteristics, and to assess the transferability of these relationships across ecoregions. Stream size consistently influenced regimes across all ecoregions and dimensions, whereas the influences of other factors varied considerably among ecoregions. For example, watershed urbanization and topography tended to be the most important predictors of flow conditions in PD streams, whereas carbonitic geology and climate tended to be the most important predictors in MT streams. Lastly, wetland land cover, climate, and topography tended to be most strongly associated with flow conditions in CP streams. Anthropogenic influences had stronger influences on flow duration, predictability, and rate-of-change than on magnitude or frequency. Notably, duration, predictability, and rate-of-change profoundly influence riverine biota but are not addressed by common streamflow regulations like minimum- or mean-flow management standards. Contrary to predictions, PD streams were not hydrologically intermediate to MT and CP streams. Rather, they exhibited the most-variable base-flow magnitudes, most-frequent yet shortest-lasting high-flow events, and flashiest hydrographs of any ecoregion. My results suggest that attempts to model and manage flow should account for all flow dimensions, given their presumably strong influence on fish ecology and evolution, but should also account for substantial differences in landscape-flow-ecology relationships among ecoregions.

INDEX WORDS: Stream hydrology, Flow regime, Urbanization, Dams, Ecoregion

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CHAPTER 1

INTRODUCTION

Flow Regime

Human exploitation and manipulation of river systems have long been known to be major factors in the loss of freshwater biodiversity (Hughes and Noss 1992, Allen and Flecker 1993). Most historical emphasis for river management was placed on ensuring minimum flows and adequate chemical water quality, whereas more recent research has shown the importance of a holistic view—considering many dimensions of the natural flow regime, for maintaining the chemical, physical, and biological conditions of rivers (Bunn and Arthington 2002, Lytle and Poff 2004). By accounting for causes of flow regime variation among rivers, we can better understand the habitat requirements of native species and forecast species that may be at risk.

Flow regime can be broken down into five key dimensions of flow: magnitude, frequency, timing, duration, and rate of change. Magnitude refers to the amount or the availability of water flowing downstream at a given time. Frequency is how often specific hydrologic conditions such as droughts and floods occur. Timing refers to when in the year certain water conditions such as droughts and floods occur. Duration refers to how long those conditions persist. Finally, rate-of-change is analogous to "flashiness", a measure of how quickly rivers rise and fall during and after precipitation events (Richter et al. 1996). At equilibrium, any stream or river possesses a characteristic flow regime, which can be categorized by calculating the mean and variance of magnitude, frequency, timing, duration, and rate-of-change across a series of hydrologic years. The flow regime is one of the most important variables in river ecosystems, as it strongly influences habitat conditions, and therefore the occurrence, fitness, and persistence of stream biota (Poff 1997, Poff et al. 1997).

The purpose of this study was to rank the relative importance of various landscape factors for predicting the five dimensions of streamflow, and to assess the transferability of these relationships across ecoregions. In the paragraphs that follow, I explain the rationale for focusing on ecoregions and elaborate on other potentially influential landscape factors, which fall into four broad categories: stream size, climate, flow regulation, and watershed land use.

Ecoregion

Ecoregions are mapped regional breaks based on characteristics of geography and differences in ecosystems (Omernik 2004). Areas with ecosystems that are similar are often found in similar latitudes and continental locations —which is why the locations of ecoregions are not haphazardly placed. Ecoregion boundaries are created based on the geology, soil type, land cover (vegetation type), land surface form, climate, and geomorphology of the region (Omernik 1987). Ecoregions are useful for ecological prediction because they holistically and simultaneously consider many different sources of environmental variability, allowing one to make and test ecological predictions within environmentally homogeneous areas. Ecoregions were designed in part with the United States Environmental Protection agency (EPA) to help regional entities develop ecological frameworks based on agreed factors (Omernik 1987). Failing to account for ecoregion boundaries may complicate attempts to transfer ecological models across geographic areas. Ecoregional boundaries have been used to assess the integrity of communities through developed tools like the "Index of Biotic Integrity" created for Virginia freshwater streams (Smogor and Angermeier 2001). To my knowledge, there is no prior research that has explicitly asked how flow-ecology relationships differ between upland and lowland streams, particularly in the Southeastern United States (SE US). This is significant because streams located in ecoregions below the fall line of the SE US are physically and chemically different from those of upland regions (Smock and Gilinsky 1992). Lowland streams have a low gradient with sandy substrate, in comparison to upland streams with gravel or cobble substrate. Lowland regions are distinguishable from upland regions due to their flat topography, low hydraulic gradients, and shallow groundwater.

This study will focus on flow regime components in relationship to ecoregion. Considering the flow regime is the master variable regulating habitat and biota in streams, I posit that ecoregion membership could be mediating relationships between the flow regime and other aspects of the environment like climate, land-use, stream-size, and dam regulation. I focused particularly on membership in seven EPA level III ecoregions in the southeastern U.S.: Southern Coastal Plain, Middle Atlantic Coastal Plain, Southeastern Plains, Piedmont, Northern Piedmont, Ridge and Valley, and Blue Ridge (Figure 1). Based on analyses of similarity and dissimilarity of these ecoregions, they were subsequently collapsed into three larger ecoregion groups: “upland” (Blue Ridge, Ridge and Valley), “lowland” (Southern Coastal Plain, Middle Atlantic Coastal Plain, and the Southeastern Plains), and “piedmont” (Piedmont, and Northern Piedmont). I hypothesize not only that the prevalence of certain landscape characteristics (e.g., geological features, climate, land uses) varies among ecoregions, but also that the relative influence of these features on hydrology will vary among ecoregions. For example, if dams are a more prominent feature of upland as opposed to lowland streams, then impoundment may play a greater role in mediating hydrology in those areas. Stratifying by ecoregion also helps me to account for factors that vary geographically, but that I did not directly index, such as stream geomorphology, soil type, and vegetation (Bailey 2014).

Stream Size

Stream size can be measured many ways, but most often is measured as the watershed area upstream of a given longitudinal location. Ecoregion-specific regional curves have been developed using regression analyses to determine the relationship between drainage area and stream width, depth, and bankfull stage (Foster 2012). As stream size increases, more open canopy leads to greater autotrophic production, meaning that energy inputs are greater further downstream. Species richness of fish and macroinvertebrates also increases from upstream to downstream in relation to increased energy production and diversity of habitat (Horwitz 1978, Vannote et al. 1980, Schlosser 1982). Smaller streams respond more drastically to individual precipitation events, and generally have exacerbated responses to land use, whereas larger rivers are less flashy and have greater flood magnitudes and durations (Scott et al. 2019, Royall 2021). Magnitude is largely determined by the size of the watershed area in which it is associated. Stream size increases as stream order increases, along with the addition of overland flow and infiltrated groundwater (Horton 1945, Nimmo and Shillito 2023).

Climate

Climate can be defined as the interaction of all atmospheric processes at a specific location, or the summation of weather over a specific period (Thornthwaite 1948). Latitude, elevation, position in reference to the ocean, and local geographic features all impact the climate of a location. Climate strongly influences hydrology through its influence on precipitation, which drives patterns of runoff and groundwater infiltration (Huff and Changnon 1964, Blöschl and Montanari 2010). Climate also comprises the temperature regime of a location, which influences evapotranspiration rates, and therefore rates of groundwater flux and stream drying (Pratap et al. 2022). Climate interacts with various other factors (e.g., topographic relief, watershed area, soil type, geology) in determining the characteristic water cycle and flow regime of an area. These characteristics vary by ecoregion and their locations, and the consideration of so many geomorphologic characteristics explains why ecoregion is such a powerful variable when considering the flow regime of a given location (Allen 2003, Werndl 2016). Understanding the relative influence of local climate on hydrology is critical when considering the potential hydrologic impacts of anthropogenic climate change and forecasting consequences for aquatic biota.

Flow Regulation

As of 2024, there are 92,075 dams in the United States (U.S.) according to the U.S. Army Corps of Engineers National Inventory of Dams (NID) (NID 2024, https://nid.sec.usace.army.mil/#/). These dams or impoundments vary in purpose, including hydroelectric, water supply, flood risk reduction, recreation, and irrigation (NID 2024). In an effort to protect against flooding, create electricity, and regulate water, we have modified flow regimes to meet our needs, and in turn disrupt natural flow regimes and their associated ecosystems. More than half the river systems across the globe are impounded (Nilsson et al. 2005). Poff et al. (2007) described how dam operations typically have a homogenizing effect on natural flow regimes. The flood pulse determines the frequency and magnitude of top-of-bank events and is a vital part of ecosystem productivity (Junk et al. 1989). Flow regulation disrupts associated flood pulses and alters ecosystems. Reservoir dams alter the magnitude, frequency, and duration of high and low flow events, irrigation-related dams alter the seasonality of flows, and hydroelectric dams alter flow periodicity (Poff et al. 2010, Ruhi et al. 2018, Zhang et al. 2018). Most related research has focused on larger, single dams, leaving the impacts on smaller order streams and cumulative impacts understudied. However, Ruhi et al. (2022) found that dams had a cumulative impact on the Colorado River, and smaller tributaries entering downstream were not able to reset natural regimes. Local conditions and the properties of dams (size, storage capacity etc.) directly impact flow regimes (Barbarossa et al 2020, Chalise et al. 2021). I hypothesize that the size of a dam and its distance upstream from a site will influence how much that dam influences site hydrology, and moreover that the cumulative hydrologic influences of a number of small or nearby dams could be just as large as the influence of a larger, more distant dam. However, such influences are poorly investigated.

Watershed Land Use

Nedd and Anandhi (2022) indicate that the population of the Southeastern United States has increased by approximately 2.59% annually from 1959 to 2012. Urban and agricultural land change will continue to increase with the population, in turn impacting the flow regimes in associated watersheds. Table 1 indicates the percentage of each ecoregion (across the entire range) that has experienced anthropogenic change. Alteration of natural land cover can impact every dimension of flow (Qian 1983, Nielsen 1986, Bruijnzeel 1990). Changes in land cover affect the hydrologic relationship between rainfall, evaporation, and the runoff response of the area in focus (Costa and Foley 1997). Urbanization increases overland flow and in turn increases the frequency, timing, and magnitude of flood events (Hollis 1975). The magnitude and timing of peak flows are especially important because they maintain the vital connection between riparian areas and the floodplain (Lytle and Poff 2004, Naiman et al. 2005). Streams with increased imperviousness across their watershed area also generally exhibit higher flood magnitudes, as well as shorter flood duration (Paul and Meyer 2008). Land cover type is also directly related to the rate of change of flows (Schoonover et al. 2006). A review of 94 studies conducted by Bosch and Hewitt (1982) found that deforestation nearly always leads to increased flow magnitude, whereas the reforestation of open land reduces flow magnitude. Historically, the level III ecoregions of focus in this study have been impacted in different ways across their entire range. I used the Land Cover Trends

Dataset (1973-2000, published 2014) to compare land use across ecoregions. Between 1973 and 2000, mountain ecoregions (Ridge and Valley, Blue Ridge) showed relatively little land cover change (USGS 2014). Piedmont ecoregions (Piedmont, Northern Piedmont) experienced rapid development that largely took place on previously forested land. Coastal Plain ecoregions (Atlantic Coastal Plain, Southeastern Plains, Southern Coastal Plains) also experienced rapid development as well as increased silviculture. Much of the forested cover in Coastal Plain regions was managed pine, which differentiates it from normal hardwood forested Piedmont cover (Land Cover Trends Dataset 2014, Sayler et al 2016). As with other environmental factors I have considered, historical land-use changes have varied widely among ecoregions of the southeastern U.S., suggesting that land-use-hydrology relationships might also vary among ecoregions.

Purpose of the study

Against that backdrop, the overall goal of my thesis was to increase our understanding of how each of these five major factors (ecoregion, stream size, climate, flow regulation, and land use) influence the five key dimensions of the flow regime (magnitude, frequency, duration, timing, and rate-of-change). I was particularly interested in testing whether and how flow-ecology relationships were mediated by ecoregion membership, especially in upland versus lowland environments. To that end, I developed a set of general and more specific hypotheses regarding ecoregion-specific flow-ecology relationships. First, I generally predicted that ecoregional flow regimes would "sort out" into two distinct hydrologic types, an upland and lowland group, with piedmont streams being intermediate. Second, I generally predicted that, holding the effects of other factors (e.g., stream size, land use) constant, lowland ecoregions would exhibit greater flood magnitudes, more frequent low flows, greater durations of low and high flow events, and slower rates of change—considering that lowland streams are characterized by low topography, pronounced flow regime variation, and more extreme weather variation (Smock and Gilinksy 1992, Marion et al. 2015). In contrast, I hypothesized that upland ecoregions would exhibit lower flood magnitudes, less frequent low flows, shorter durations of low and high flow events, and greater rates of change associated with low and high flow events, given that upland streams are found at higher elevations, have less extreme weather variation, and tend to have more uniform stream channels that are typically flowing (Marion et al 2015). Fourth, I predicted that spatial variation in lowland hydrology would be best explained by ecoregional differences in temperature, topography, and precipitation, rather than by urban or agricultural land use. In contrast, I hypothesized that developed and agricultural cover would be important in explaining flow regimes in piedmont and mountain streams. Fifth, I predicted that drainage area (or stream size) would be an important predictor of hydrology across ecoregions and flow dimensions. In reference to environmental impacts, larger rivers often experience the cumulative impacts of alteration across their watersheds (Poff et al. 1997). I also made a number of more specific predictions, which are summarized in Table 2. I tested these hypotheses by compiling and analyzing long-term stream flow data collected from streams throughout the southeastern U.S. Results provide insight into which environmental factors, both natural and anthropogenic, most strongly regulate which aspects of hydrology, and how well these relationships translate from mountain to lowland ecoregions.

Table 1. Level III Ecoregional Land Categories in 2000 (USGS, Land Cover Trends Project 2014)

Ecoregion	% Developed	% Agriculture	% Forest	% Wetland
Piedmont	16.4	23.1	55.1	0.7
Northern Piedmont	27.3	34.4	35.4	0.7
Mid. Atl. Coastal Plain	9.0	22.7	32.1	24.6
Southern Coastal Plain	20.8	7.9	24.0	20.4
Southeastern Plains	10.3	21.5	51.8	10.3
Ridge and Valley	9.3	30.4	55.8	0.7
Blue Ridge	7.2	13.7	78.3	0.0

Table 2. Hypotheses by flow dimension

Flow Dimension	Predictor(s)	Response	Explanation
Magnitude	1. Median daily flow (ma2) 2. CV of daily flow (ma3)	1. (-) Agricultural and developed cover (all ecoregions) 2. (-) CP flow regimes	1. Land use increases baseflow (Bosch and Hewlett 1982) 2. CP is often close to groundwater table, increased wetland presence will reduce CV of daily flows
Frequency	1. Low flow (fl3) 2. High flow (fh7)	1. (-) Agricultural and developed cover (MT and PD) 2. (+) Upstream precipitation and upstream temperature range (PD only)	1. Land cover change causes more frequent flooding, where CP streams show resiliency 2. High development in PD watersheds will increase the impacts of weather (less shading and more overland flow)
Duration	1. Low & high flow (dh15, dl16) 2. Low flow (dl16)	1. (+) Flow regimes (CP only) 2. (-) PD flow regimes (PD only)	1. Flatter topography and decreased flashiness in PD streams will lead to longer durations 2. Overland flow caused by increased development will reduce the duration of low flow events

Timing	1. Low flow timing (tl2) 2. Low flow timing (tl2)	1. (-) Agricultural cover, (-) developed cover 2. (+) Upstream precipitation, (+) upstream temperature (all ecoregions)	1. Changes in soil infiltration may alter seasonal low-flow events 2. Lack of water is likely related to seasonal precipitation and weather
Rate-of-Change	1. Flashiness (ra8) 2. Flashiness (ra8), flow rise (ra1_div_ma2)	1. (-) CP streams 2. (+) Development and agricultural cover (PD and MT)	1. CP hydrology 2. Specific to developed and agricultural cover across ecoregional groups

CHAPTER 2

METHODS

Study Area

The area of focus for the study included the Southern Coastal Plain, Middle Atlantic Coastal Plain, Southeastern Plains, Piedmont, Northern Piedmont, Ridge and Valley, and Blue Ridge EPA level III ecoregions of Georgia, South Carolina, North Carolina, and Virginia (Figure 1). These states were chosen because of their similar ecoregion compositions, geologies, and biogeographic histories. The Appalachian Plateau ecoregion was left out of analyses due to the lack of gages with historical datasets. For example, there are not any USGS stream gages in the Appalachian Plateau of Georgia, and no other states of focus in the study area occur within that ecoregion. The Northern Piedmont ecoregion of Virginia was included in analyses as it had 12 gages that met selection criteria and was not found to be statistically different from the Piedmont (level III) ecoregion.

Streamflow Data

Streamflow data were downloaded from the United States Geological Survey (USGS's) network of hydrologic gages (https://waterdata.usgs.gov/nwis/rt). Each gage was considered a member of the ecoregion in which the majority of its upstream watershed area was located. Within the states and ecoregions described above, for inclusion in the study, I included sites with stream gages that have been in place a minimum of 30 years, with no more than two non-consecutive years of missing data within that period. All gages selected had a drainage area of less than 7,770 square kilometers. Approximately 30 years of gage data are necessary to have enough statistical power for hydrologic analyses (Kennard et al. 2010). To characterize the flow regime of each gage location, I calculated a series of hydrologic metrics using the "EflowStats" package from the USGS R archive network and the "Hydroecological Integrity Assessment Process," (Olden and Poff 2003, Henriksen et al. 2006, Archfield et al. 2013). Each of the five dimensions of the flow regime was indexed by two different metrics, for a total of 10 metrics calculated for each gage. Metrics were chosen based on presumed meaningfulness to riverine biota. Magnitude was indexed by calculating median daily flow (ma2) and the coefficient of variation of daily flows per year (ma3). Frequency was indexed by calculating numbers of low-flow (fl3) and high-flow events per year (fh7). Timing was indexed by calculating the CV of timing of low flows (tl2) and the Colwell's predictability of flows (ta2) (Colwell 1974). Duration was indexed by calculating the duration of low flow events (dl16) and the duration of high flow events (dh15). Lastly, rate of change was indexed by calculating the steepness of flow rise relative to magnitude (ra1 divided by ma2; henceforth "ra1_div_ma2") and number of days per year featuring reversals of hydrograph direction (ra8) (Table 3, Olden and Poff 2003, Henriksen et al. 2006, Archfield et al. 2013). Variable ra8 is defined by Richter et al. (1996) and Olden and Poff (2003) as an indicator of hydrologic alteration.

Environmental Data

As of 2024, there are 14,096 dams in the study area for this project. At the point this study began in 2021, there were 13,628 dams in the study area (an increase of 468 dams in four years). Considering this, the impact of flow regulation on a given USGS flow gage was accounted for through the development of a novel index. The USGS Streamstats Batch Processing Tool (https://www.usgs.gov/tools/streamstats-batch-processing-tool) was used to create upstream watershed area SHP files and capture stream size for each USGS gage. Stream grids were downloaded based on state/region from the USGS as directed in the tool instructions. The U.S. Army Corps of Engineers (USACE) National Inventory of Dams was used to source dam locations in the watershed and to determine the dimensions of each dam. Dams were then snapped to the existing stream grid in ArcGIS (ESRI 2011). Streamline distances were used to calculate dam distance to each USGS gage. Then, for any identified dam in the watershed upstream of a gage, impact was calculated as the square root of the area of the dam divided by the fluvial distance from the gage to the dam (km). The total impact of all upstream dams on each gage was calculated as the summation of all individual impacts, where k = total number of dams in the watershed. A = area of dam (square meters). D = dam distance (km) (Table 3).

$$\text{Dam Impact} = \sum_{i=1}^{k} \left(\frac{\sqrt{Ai}}{Di} \right)$$

*Higher values indicate a larger presumed hydrologic impact of dams.

Historic rainfall, soil, and temperature data were gathered using EarthENV freshwater variables, which accesses WorldClim historic data (1970-2000), International Soil Reference and Information Centre (ISRIC) digital soil maps, and the HydroSHEDS database (Table 3, Lehner et al. 2008, Hengl et al. 2014, Domisch et al. 2015). All data sourced from EarthENV had a 1-km^2 spatial resolution. Upstream temperature range (°C x 10) (EarthENV) was selected as it captures climatic variability, where the minimum upstream temperature of the coldest month is subtracted from the maximum upstream temperature of the warmest month. Annual upstream precipitation (mm) (EarthENV) was selected to measure the impacts of precipitation on hydrology in each watershed. Average soil cation exchange capacity (cmol/kg) (EarthENV, ISRIC) was selected to measure the impact of soils and geology on stream hydrology. Average slope (degrees x 100) (EarthENV, HydroSHEDS) and average elevation (m) (EarthENV, HydroSHEDS) of each watershed were also included in the dataset, Average altitude of each gage (feet above NAVD88) was collected from USGS for each stream gage (this variable can also be defined as the elevation of the gage at 0.0 ft. gage height, also referred to as "gage datum").

Land cover class data were gathered from the 2016 National Land Cover Database (NLCD) and combined with upstream watershed SHP files to generate cover type calculations (USGS 2016). There were two versions of land cover variables used in this study: land cover proportions from the year 2001, and "change" in land cover proportions from 2001 to 2016. Within the two versions, various NLCD land cover types were combined into additional groups. Developed cover types 22, 23, and 24 were combined into a new developed cover grouping (Developed_2001, APPENDIX I). Forested cover types 41, 42, and 43 were combined into a new forested cover grouping (Forested_2001). Agricultural cover types 81 and 82 were combined into a new agriculture grouping (Agriculture_2001), and wetland cover types 90 and 95 were combined to create a new wetland cover grouping (Wetland_2001). Cover type 11 was selected to capture open water features (Open_water_2001) and was not grouped with any other cover types. These same cover type groupings were used to measure the change in the proportion of land cover from 2001 to 2016, and instead begin with the epithet "Delta."

Environmental Flow Models

I presumed that various physiographic/topographic factors, including gage altitude, upstream watershed elevation, and upstream watershed slope, all would potentially influence hydrology, but these three variables were strongly correlated (altitude vs elevation $r = 0.95$, altitude vs slope $r = 0.77$, elevation vs slope $r = 0.89$). I therefore used principal components analysis (PCA) in *R* using the *vegan* package to reduce the dimensionality of these phenomena into a single ensemble variable (Oksanen et al. 2022). The first axis resulting from this PCA explained 92% of the overall variation, was positively associated with all three input variables (loadings for datum = 0.58, elevation = 0.60, and slope = 0.56), and was retained for subsequent analyses and named "Montane_PCA". Larger values of this variable indicate more-montane conditions at and upstream of a stream gage, whereas smaller values indicate more-lowland conditions.

Given the limited sample sizes of gages in some ecoregions (e.g., 9 in the Southern Coastal Plain, 22 in the Middle-Atlantic Coastal Plain), I combined some ecoregions into larger ecoregion groups for further analyses. I first analyzed hydrologic similarity among ecoregions to determine which ecoregions would form hydrologically homogeneous groups and be appropriate to combine. Using the 10 hydrologic indices, I calculated Bray-Curtis distances, and from these distances used the *adonis* function in the R package *vegan* to conduct permutational multivariate analysis of variance (PERMANOVA) among ecoregions (6 ecoregions, 9999 permutations) (Oksanen et al. 2022). Because the global model was significant ($P < 0.0001$), I then tested all possible pairwise comparisons using the *pairwise.adonis* function in the *pairwise.adonis* package (Table 4, Martinez 2020). These tests indicated that Piedmont stream hydrology was significantly different from coastal and mountainous regions, but Piedmont streams were not significantly different from streams in the Northern Piedmont. Pairwise comparisons revealed that level III Ridge and Valley streams were statistically different from Blue Ridge streams. Additionally, Ridge and Valley regimes were not statistically different from Northern Piedmont, Southeastern Plains, or Southern Coastal Plain regimes. Based on this backdrop, I combined gages into three ecoregion groups: mountain or "MT" (Blue Ridge and Valley and Ridge), coastal plain or "CP" (Southeastern Plains, Mid-

Atlantic Coastal Plain, and Southern Coastal Plain), and piedmont or “PD” (Piedmont and Northern Piedmont). Another permutational multivariate analysis of variance (PERMANOVA) was conducted which provided statistical justification of the new groupings (full model $p < 0.0001$, pairwise comparisons adjusted.p < 0.003 for all 3 groups). The combination of statistically significant level III ecoregions was necessary due to limited sample sizes, and likely contributed to the artificial inflation of the variance of the MT grouping, which as a result, potentially reduced the explanatory power of the new ecoregional groupings.

I used redundancy analysis (RDA) to jointly investigate the relative association of each of the 16 candidate environmental predictors with the flow regime at each gage, as indexed by the 10 hydrologic indices. This approach seeks to find the most parsimonious subset of predictors that constrains variation in the multivariate response. I fit optimal models using stepwise variable selection (*ordistep* function in *vegan*) with 1000 permutations and alpha thresholds of 0.05 for variables entering and leaving the model (Oksanen et al. 2022). Four separate RDA models were run, one including all ecoregions and one for each of the three ecoregion groups separately. I assumed that environmental variables retained by the RDA, particularly if loading heavily onto the ordination and/or loading in a direction showing ecoregion group separation, were importantly associated with stream flow.

I complemented RDA models with an additional technique that sought to quantify the relative form and magnitude of influence of each predictor variable on each hydrologic index, while statistically accounting for the influences of all other predictors variables. This allowed me to, for example, assess the influence of urban land cover on flow magnitude in PD while holding influences of stream size and dams constant. Specifically, I used random forest (RF) regression models, which allow inclusion of both continuous and categorical predictor variables, explicitly account for variable interactions, and are robust to nonlinear and nonadditive relationships, variable collinearity, and non-normality (Liaw and Weiner 2002). Environmental predictor correlations are outlined in APPENDIX II. RF analyses aimed to identify the optimal model or "tree" that explained the variation in a response variable based on candidate environmental predictor variables (De’ath and Fabricius 2000). The model tree underwent splits at "nodes," representing binary splitting of specific predictor variables. These variables were chosen to minimize the within-group sum-of-squares for a given hydrologic response variable. Predictor variables frequently selected as high-level splitters can be considered important in explaining the variation in the response variable. Unlike the related technique CART, RF generates multiple trees by partitioning random subsets of the data to find recurring patterns between response and predictor variables, instead of building a single model using the entire dataset. The slight variations in each tree help determine which predictor variables are more important and should be included in the final model. RF helps prevent model overfitting by integrating multiple trees developed with unique bootstrapped samples from the entire dataset (Cutler et al. 2007). A combination of the *caret* (Kuhn 2008) and *randomForest* (Liaw 2002) packages in *R* were utilized for RF modeling. I set the number of randomly sampled variables per split (*mtry*) to 4, sampled 5000 total trees, and used 10-fold cross-validation to measure model accuracy. Variable importance was determined by calculating the percent increase in model mean square error (%incMSE) when that variable was randomized (i.e., higher %incMSE indicates that a variable explains more variance). For comparison across models, I then standardized %incMSE to range from 0 (least important) to 100 (most important) within any given model. Throughout this paper, variable "importance" refers to the ranking of standardized %incMSE across predictors for a given response. There are no defined criteria for how high the RF importance score should be to count as a biologically important relationship. I treated any variable with an importance score ≥ 70 (i.e., at least 70% as important as the most important variable) as worthy of interpretation. For environmental summaries based on the proportion of models in which a certain predictor was important, flow dimension proportions ≥ 0.33 were considered important, and for ecoregional proportions ≥ 0.30 was considered important. Furthermore, for the top three most important predictors for each response variable in each ecoregion, I used partial dependence plots (PDPs) to visualize univariate relationships. These PDPs showed predicted variation in a response variable (e.g., hydrologic variable ma2) as a function of a predictor variable (e.g., Drainage_area) while holding all other predictor variables constant. Models were run separately for each of the 10 response variables for each of the 3 ecoregion groups, for a total of 30 RF models.

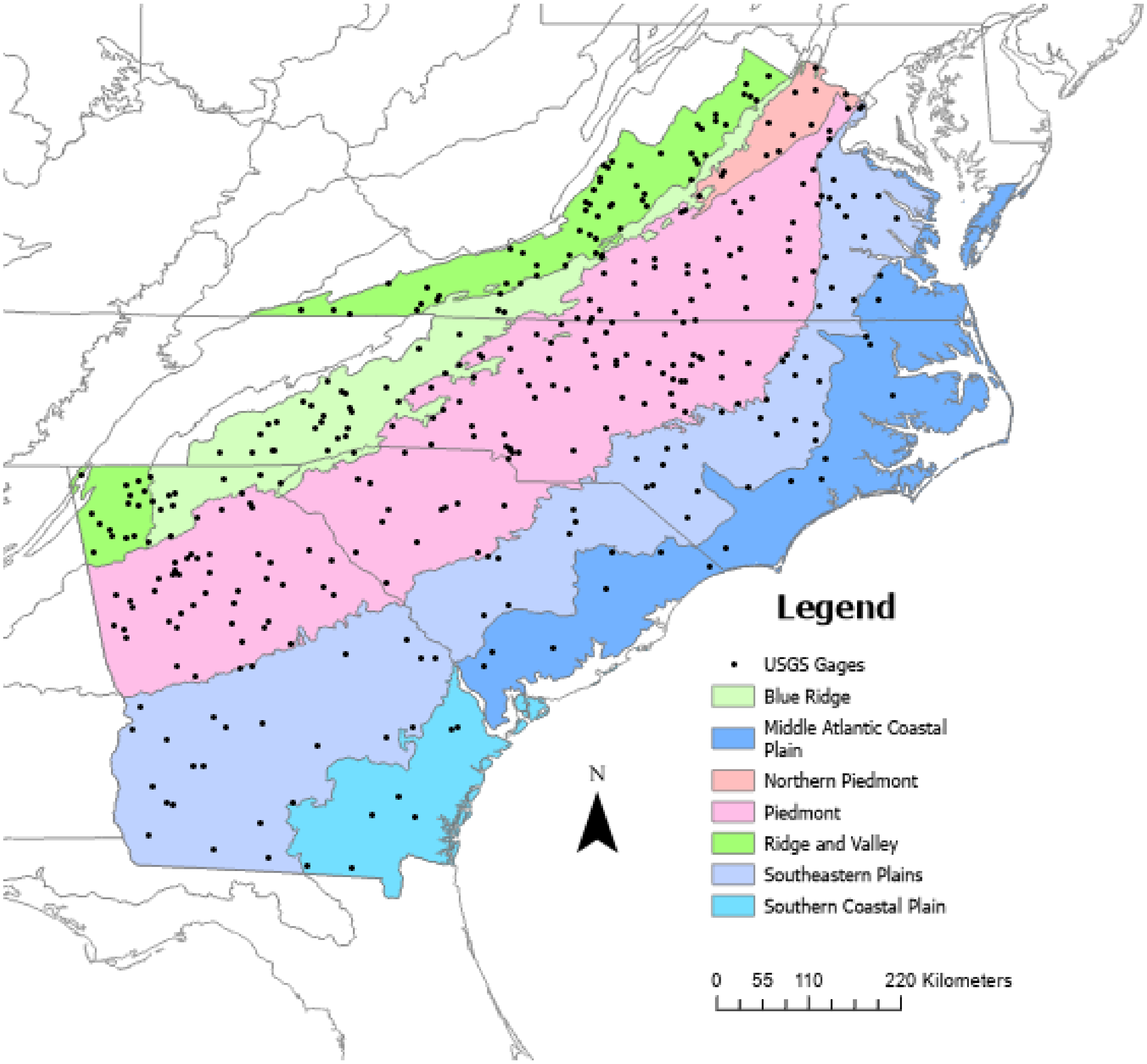

Figure 1. Map of all 375 gages across level III ecoregions and U.S. states of focus. For analyses, Blue Ridge and Ridge and Valley were combined into the "MT" ecoregional group, Middle Atlantic Coastal Plain, Northern Piedmont, and Piedmont were combined into the "PD" group, and Southeastern Plains and Southern Coastal Plain were combined into the "CP" group.

Table 3. Environmental and hydrologic variables (including definitions and sources) used in this study.

Variable Type	Variable ID	Definition	Source
Magnitude	ma2	median daily flow	1
Magnitude	ma3	CV of daily flows within a year, averaged across years	1
Frequency	fl3	average number of events per year with flow <5% of all year mean	1
Frequency	fh7	average number of flow events per year > 7x median all years	1
Duration	dl16	# of days < 25th%, averaged across years	1
Duration	dh15	# of days > 75th%, averaged across years	1
Timing	tl2	Variability (CV) in Julian date of annual low flows.	1
Timing	ta2	Predictability (ex. Colwell 1974): (1-(uncertainty with respect to interaction of time and state - uncertainty with respect to time /log (number of state)	1
Rate-of-change	ra1_div_ma2	(change in cfs/day during days of positive change)/ma2	1
Rate-of-change	ra8	# of days per year in which flow changes direction	1
Dam Regulation	Dam	$Impact = \sum_{i=1}^{k} \frac{\sqrt{Ai}}{Di}$ k = total number of dams in watershed A = area of dam (square meters) D = dam distance (km)	2
Climate	Temp_range	Upstream temperature annual range (Max_temp - Min_temp) (°C x 10)	3
Climate	Annual_precip	Annual upstream precipitation (sum in mm)	3
Soils	Soil_cation	Soil cation exchange capacity (average, cmol/kg)	3
Physiography	Montane_PCA	Topographic index - PCA1 of gage datum, elevation, and slope measurements	3
Land Cover	Open_water_2001	Proportion of open water cover (11) in the watershed (year 2001)	4
Land Cover	Developed_2001	Proportion of all developed land cover types (22, 23, 24) (year 2001)	4
Land Cover	Forested_2001	Proportion of all forested land cover types (41, 42, 43) (year 2001)	4
Land Cover	Agriculture_2001	Proportion of all agricultural land cover types (81, 82) (year 2001)	4
Land Cover	Wetland_2001	Proportion of all wetland land cover types (90, 95) (year 2001)	4
Land Cover	Delta_open_water	The change in open water cover from 2001 to 2016 (as a proportion)	4
Land Cover	Delta_developed	The change in total developed cover from 2001 to 2016 (as a proportion)	4
Land Cover	Delta_forested	The change in total forest cover from 2001 to 2016 (as a proportion)	4
Land Cover	Delta_agriculture	The change in total agricultural cover from 2001 to 2016 (as a proportion)	4
Land Cover	Delta_wetland	The change in total wetland cover from 2001 to 2016 (as a proportion)	4
Physiography	Drainage_area	The upstream drainage area (km2)	5

Source key: 1 = (Henriksen et al. 2006, Archfield et al. 2013, Olden and Poff 2003), 2 = Internally developed, 3 = EarthENV, 4 = NLCD Land Cover Trends Database (2001), 5 = StreamStats Batch Processing Tool

Table 4. Level III ecoregion PERMANOVA pairwise comparisons. Response variable is Bray-Curtis distance based on 10 hydrologic variables.

	PD	**N. PD**	**S.E. Plains**	**M.A. CP**	**S. CP**	**BR**	**R&V**
PD	-	0.080	**0.001**	**0.001**	**0.002**	**0.001**	**0.001**
N. PD	1.000	-	**0.003**	**0.001**	**0.001**	**0.001**	**0.004**
S.E. Plains	**0.021**	0.063	-	**0.028**	**0.033**	**0.001**	**0.004**
M.A. CP	**0.021**	**0.021**	0.588	-	0.328	**0.001**	**0.001**
S. CP	**0.042**	**0.021**	0.693	1.000	-	**0.001**	**0.003**
BR	**0.021**	**0.021**	**0.021**	**0.021**	**0.021**	-	**0.001**
R&V	**0.021**	0.084	0.084	**0.021**	0.063	**0.021**	-

*Bonferroni adj. p-values are below the diagonal, and p-values are above the diagonal.
*Bold values indicate p-values or adjusted p-values < 0.05

CHAPTER 3

RESULTS

The filtering process for gage selection began with 405 gages in Georgia, 262 in South Carolina, 290 in North Carolina, and 256 in Virginia. After filtering for focal ecoregions and data sufficiency, the final dataset consisted of 375 gages, including 112 in MT, 173 in PD, and 90 in CP (Figure 1). Summary statistics were calculated per ecoregion indicating the mean, standard deviation (SD), and range of each environmental variable (Table 5).

The RDA model including all ecoregion groups (375 gages) explained 54.2% of the variance (constrained inertia) of the 10 hydrologic indices based on a model-selected subset of 10 of the 16 candidate environmental predictors (APPENDIX III and IV). The first two RDA axes explained 46.6% of this constrained inertia. The first axis primarily was positively associated with stream size (Drainage_area) and dams (Dam) and negatively associated with upstream annual temperature range (Temp_range), whereas the second axis primarily was positively associated with wetlands (Wetland_2001) and agriculture (Agricultural_2001) and negatively associated with topography (Montane_PCA) (Figure 2). Based on these first two axes, larger streams were associated with greater average baseflow magnitude (ma2) and more-predictable seasonal variation (ta2), whereas smaller streams were associated with more-variable baseflow magnitude (ma3), more-frequent high (fh7) and low flows (fl3), and steeper rate-of-change (ra1_div_ma2). Streams in CP exhibited longer-lasting high (dh15) and low flows (dl16), PD exhibited more-frequent hydrograph reversals (ra8), and MT was intermediate in most regards. In terms of land use, CP featured more wetland cover, PD featured more development, and MT was again intermediate. I hypothesized that regimes would “sort out” into two distinct hydrologic types (upland and lowland) with PD streams being intermediate. PD and MT flow regimes exhibited some overlap in the global “All ecoregions” RDA model, but PD streams were not intermediate along a gradient between upland and lowland groupings. CP streams were clearly separated from MT and PD streams along axis RDA2, but PD and MT streams exhibited unexpected overlap and sorted along axis RDA1. MT streams were associated with increased stream size, (Drainage_area), predictability (tax2), and median daily flows (ma2). PD streams were associated with increased CV of daily flows (fh7), flow rise (ra1_div_ma2), and low flow frequency (fl3).

I also analyzed each ecoregion group individually in separate RDAs, to assess whether the flow regimes of different ecoregions tended to associate with different environmental factors (Figure 2, APPENDIX III and IV). The best-fitting CP, PD, and MT models explained 55.2%, 63.0%, and 63.7% of the variance in hydrology using 7, 11, and 11 environmental variables, and the first two axes of these models captured 46.1%, 53.5%, and 55.9% of this explained variance, respectively. Across ecoregion-specific RDAs, Drainage_area was always retained and generally associated positively with baseflow magnitude (ma2) and predictability (ta2). In CP and PD streams, Montane_PCA was associated with more-predictable seasonal variation (ta2) and less-frequent low flows (fl3), whereas topography was not selected as important for MT streams. Variable Temp_range was important in CP and MT streams, but associations with flow were inconsistent. Soil cation exchange capacity (Soil_cation) was important only in MT streams and associated with longer-lasting high (dh15) and low flows (dl16) and less-frequent hydrograph reversals (ra8), whereas in CP streams soil cation exchange capacity (Soil_cation) was not selected as important. Developed land use (Developed_2001) was most important in PD and associated positively with more-frequent hydrograph reversals (ra8) and shorter-duration low (dl16) and high flows (dh15). Watershed development was less important in CP and not selected in the MT model. Likewise, forested land use (Forested_2001) was important only in PD and its association was opposite that of development.

I built a total of 30 RF models to test and rank the importance of 16 candidate environmental variables for predicting hydrologic indices in each of the three ecoregion groups (Tables 6-10). Model R^2, determined by 10-fold cross-validation, ranged across models from 0.31 (ra1_div_ma2 in CP) to 0.86 (ma2 in MT), averaging 0.59 across all models. Model R^2 was similar among ecoregion groups, averaging 0.56, 0.63, and 0.58 in CP, PD, and MT models, respectively. On the other hand, regardless of ecoregion, models predicting magnitude tended to feature a higher explanatory power (mean R^2 = 0.74) than models predicting frequency (0.55), duration (0.59), timing (0.51), or rate of change (0.54). The relative importance of environmental variables for predicting hydrology varied widely among ecoregions and hydrologic indices, as detailed below.

Magnitude – Regardless the ecoregion group, the most important predictor of median daily flow (ma2) was Drainage_area (Table 6). In all ecoregions, ma2 increased nearly linearly as Drainage_area increased (Figure 3). Relative to Drainage_area, which featured an importance score of 100 for ma2 in all three ecoregions, no other predictors were nearly as important (i.e., none featured an importance score > 44). However, the dam impact index (Dam) was one of the top-three predictors for all ecoregions, and in each case, ma2 increased with increasing flow regulation. The CV of daily flow magnitude (ma3), in contrast, was influenced by a wider variety of factors, which differed more among ecoregion groups (Table 6). In CP and MT, the most important predictor of ma3 was Temp_range, but the directions of relationships were opposite: negative in CP, positive in MT (Figure 4). The most important predictors of ma3 in PD were Montane_PCA, Annual_precip, and Drainage_area, all being negatively related to ma3. This indicates that in PD, intra-annual flow variability decreased as precipitation, topography, and stream size increased. Variable ma3 also decreased with Montane_PCA in CP, with Upstream annual precipitation (Annual_precip) and Drainage_area in MT, and increased with agricultural land use in CP.

Frequency – The most important predictors of low flow frequency (fl3) in CP streams were Montane_PCA and Temp_range (Table 7). As topography decreased, fl3 increased (Figure 5). Variables Drainage_area and Montane_PCA were the most important variables in the PD. As both increased, the fl3 decreased. Drainage_area was the most important predictor of low flow frequency in the MT, where the frequency of low flows fl3 decreased as Drainage_area increased. The change in development in MT streams was negatively related to the fl3. There were seven different important predictors of high flow frequency (fh7) in CP streams (Table 7). Variables Annual_precip and Wetland_2001 both had positive relationships with fh7 (Figure 6). As fh7 decreased, Annual_precip and Wetland_2001 increased. The frequency of fh7 and Temp_range exhibited a non-linear relationship. Additionally, changes in open water (Open_water_2001) and Wetland_2001 were both important drivers of fh7 in CP streams. This was the only instance where a variable associated with change in land cover exceeded an importance score of

70. Variable Developed_2001 was also an important driver of fh7 in the CP. Montane_PCA and Developed_2001 were the most important predictors of fh7 in PD streams. Montane_PCA had a negative relationship with fh7, whereas developed_2001 had a positive relationship. Temp_range was the only variable with an importance score greater than 70 in MT streams. As Temp_range increased, so did fh7.

Timing – The CV of low flow timing (tl2) in CP streams was associated with different predictors than PD and MT streams, where Temp_range and Wetland_2001 were most important (though temperature range was close to ≥70 in the Piedmont) (Table 8). Variable tl2 decreased as Temp_range increased (Figure 7). As Wetland_2001 increased, so did tl2. PD and MT tl2 were both associated with dam impact (Dam) and open_water_2001, where both relationships were positive. Variable Agriculture_2001 was an important predictor of tl2 in MT streams and was unimportant in PD and CP streams. Top ranking predictors in MT streams all had positive relationships with tl2. Variable Drainage_area was the most important variable in determining hydrologic predictability (ta2) across all three ecoregional groups (Table 8). Variable Montane_PCA was a secondary predictor of predictability in CP and PD streams. Variable Temp_range was important (≥ 70) in CP streams and ranked in the top three of MT stream predictors. Coastal Plain predictability was directly related with Temp_range, and negatively related with MT predictability (Figure 8). Wetland cover (Wetland_2001) had an importance score less than 70 in CP and MT streams, but still ranked toward the top of the list of environmental variables. Wetlands reduced predictability in CP streams, and increased predictability in MT watersheds.

Duration – Drainage area was the most important predictor of low flow duration in CP streams (Table 9). Low flow duration (dl16) increased as drainage area increased. Low flow duration (dl16) in PD streams was explained by multiple land cover predictors and Montane_PCA. Variables Agriculture_2001 and Wetland_2001 both had positive relationships with dl16, while the impact of Developed_2001 had a negative relationship (Figure 9). Drainage area (Drainage_area) was the most important predictor of high flow duration (dh15) in CP streams (Table 9). Variable Wetland_2001 was second to Drainage_area. Both explanatory variables had a positive relationship with dh15 (Figure 10). Variables Developed_2001 and Open_water_2001 were important predictors of dh15 in PD streams. Variable Open_water_2001 had a positive relationship with dh15, and Developed_2001 had an indirect relationship with dh15. Variables Soil_cation and upstream Temp_range were the most important predictors of MT dh15, where both relationships were positive.

Rate-of-change – Drainage area (Drainage_area) was the most important predictor of flow rise steepness (ra1_div_ma2) in CP streams, followed by upstream Annual_precip and Temp_range (Table 10). Temp_range had a non-linear relationship with ra1_div_ma2, while Annual_precip had a negative relationship (Figure 11). Variable ra1_div_ma2 in PD streams was explained by Montane_PCA and Drainage_area, both of which had negative relationships. Variable Temp_range was the most important driver of ra1_div_ma2 in MT streams followed by Drainage_area. Variable Temp_range had a positive relationship with ra1_div_ma2, while Drainage_area had a negative relationship. Hydrograph reversals (ra8) in CP streams were explained by Wetland_2001, Drainage_area, and Montane_PCA (Table 10). Of those three predictors, Montane_PCA had a positive relationship with ra8, and the other two relationships were negative (Figure 12). Among PD streams, there were 5 explanatory variables with an importance score ≥ 70 in reference to ra8. Variables Wetland_2001 and Developed_2001 were the most important variables, followed by Agriculture_2001. Of those three, Developed_2001 was the only variable that had a positive relationship with ra8. Variable Montane_PCA and dam impact (Dam) were ranked fourth and fifth among predictors of ra8 in the PD. Variable ra8 is an indicator of hydrologic alteration, and the importance of anthropogenic impacts such as dams, agricultural cover, and developed cover in the PD (verses the other two ecoregional groups) highlights that PD hydrology was largely defined be alteration to the landscape. Soil cation exchange capacity (Soil_cation) was the only variable with an importance score greater than 70 among MT streams—this relationship was negative.

I summarized across RF models in two ways to assess broad trends. First, I asked how consistently important each environmental variable was in predicting each dimension of flow, by calculating the proportion of models for each dimension (3 ecoregion groups x 2 indices = 6 models per dimension) in which that environmental predictor had an importance score ≥70 (Table 11). Proportions ≥ 0.33 were considered to be important. Second, I asked how consistently important each environmental variable was in predicting flow characteristics in each ecoregion, by calculating the proportion of models for each ecoregion group (5 dimensions x 2 indices = 10 models per ecoregion group) in which that environmental predictor had an importance score ≥ 70. Proportions ≥ 0.30 were considered to be important (Table 12). In reference to importance proportions based on environmental variables, variables Drainage_area and Temp_range were important predictors of flow across all five flow dimensions, as both variables were important in at least 33% of all flow dimension models (Table 11). Variable Montane_PCA was a unique predictor of flow frequency and rate of change. Both variables were important in 50% of models involving their associated dimension. Variables Soil_cation and Developed_2001 were unique predictors of flow duration, as both were important in 33% of duration models. Neither variable was deemed important in any other flow dimension summary in Table 11. Dams (Dam) and Open_water_2001 were unique predictors of flow timing, and wetland cover was an important predictor of flow duration and rate of change. Dams (dam) and Open_water_2001 were important in 33% of timing models, and Wetland_2001 was important in 33% of duration and rate-of-change models. In reference to importance proportions based on ecoregional groupings, Drainage_area was an important predictor of flows across all three ecoregional groups, being important in at least 40% of all models (Table 12). Topography (Montane_PCA) was an important predictor in 40% of CP models and 60% of PD models, and Temp_range was an important predictor in 60% of CP models and 50% of MT models. Variable Wetland_2001 was only an important predictor of CP hydrology (40% of models) and Developed_2001 was only an important predictor of PD hydrology (30% of models). Variable Soil_cation was only an important predictor of MT hydrology (30% of models).

Table 5. Summary statistics describing the mean, standard deviation, min, and max of all environmental predictor variables by ecoregional grouping.

	CP				MT				PD			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Dam	36.14	64.28	0.00	522.53	39.42	89.45	0.00	534.27	72.50	274.91	0.00	3295.07
Drainage_area	1843	2023	20	7563	1108	1463	13	7167	1149	1724	7	7682
Montane_PCA	-1.53	0.21	-1.85	-0.89	1.97	1.45	-0.86	6.41	-0.48	0.80	-1.51	2.45
Temp_range	326.00	16.52	361.00	293.00	340.67	12.03	319.00	369.00	338.19	11.95	318.00	366.00
Annual_precip	2387	142	2040	2732	2542	515	1850	3798	2412	261	2006	3450
Soil_cation	12.52	1.94	10.00	23.00	16.06	3.10	11.00	22.00	11.40	1.35	9.00	18.00
Open_water_2001	0.00	0.00	0.00	0.02	0.00	0.01	0.00	0.05	0.00	0.01	0.00	0.05
Developed_2001	0.02	0.04	0.00	0.29	0.01	0.01	0.00	0.07	0.04	0.07	0.00	0.41
Forested_2001	0.20	0.09	0.04	0.47	0.36	0.11	0.11	0.64	0.30	0.12	0.00	0.60
Agriculture_2001	0.11	0.07	0.00	0.30	0.07	0.07	0.00	0.35	0.09	0.06	0.00	0.38
Wetland_2001	0.09	0.07	0.00	0.38	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.06
Delta_open_water	0.0002	0.0007	-0.0047	0.0026	0.0000	0.0003	-0.0023	0.0008	0.0003	0.0014	-0.0009	0.0180
Delta_developed	0.0023	0.0048	0.0000	0.0305	0.0016	0.0032	0.0000	0.0220	0.0060	0.0100	0.0000	0.0800
Delta_forested	-0.0067	0.0125	-0.0449	0.0396	-0.0013	0.0067	-0.0330	0.0180	-0.0090	0.0150	-0.0700	0.0380
Delta_agriculture	-0.0025	0.0037	-0.0206	0.0088	-0.0027	0.0039	-0.0280	0.0000	-0.0060	0.0050	-0.0300	0.0001
Delta_wetland	-0.0002	0.0004	-0.0018	0.0004	0.0001	0.0001	-0.0001	0.0009	0.0000	0.0000	-0.0030	0.0005

Table 6. Random Forest (RF) results for flow magnitude by ecoregion, mtry = 4, trees = 5000, 10-fold cross-validation. Predictor values ≥ 70 are considered important. Red colors indicate negative relationships, and blue colors indicate positive relationships. Darker shading indicates importance = 100, medium shading indicates 100 > importance ≥ 70, lighter shading indicates importance < 70 but still among the top three. Gray shading indicates non-monotonic relationships.

	Magnitude					
	CP ma2	**PD ma2**	**MT ma2**	**CP ma3**	**PD ma3**	**MT ma3**
R^2	0.78	0.83	0.86	0.47	0.79	0.69
Drainage_area	100	100	100	18	71	64
Montane_PCA	23	31	13	68	100	20
Soil_cation	6	0	15	8	4	47
Dam	34	44	31	30	47	16
Annual_precip	16	17	11	46	81	49
Temp_range	18	11	17	100	21	100
Forested_2001	0	13	0	31	11	25
Agriculture_2001	6	15	4	61	16	13
Developed_2001	7	18	15	24	27	9
Open_water_2001	8	25	37	0	10	8
Wetland_2001	6	18	12	43	40	21
Delta_forested	8	6	4	9	1	0
Delta_agriculture	8	9	12	17	10	6
Delta_developed	11	11	17	3	12	30
Delta_open_water	15	6	11	40	0	17
Delta_wetland	8	13	13	38	22	0

Table 7. Random Forest (RF) results for flow frequency by ecoregion, mtry = 4, trees = 5000, 10-fold cross-validation. Predictor values ≥ 70 are considered important. Red colors indicate negative relationships, and blue colors indicate positive relationships. Darker shading indicates importance = 100, medium shading indicates 100 > importance ≥ 70, lighter shading indicates importance < 70 but still among the top three. Gray shading indicates non-monotonic relationships.

	Frequency					
	CP fl3	**PD fl3**	**MT fl3**	**CP fh7**	**PD fh7**	**MT fh7**
R^2	0.45	0.53	0.38	0.49	0.78	0.69
Drainage_area	15	100	100	71	37	49
Montane_PCA	100	93	47	49	100	23
Soil_cation	16	12	9	18	0	45
Dam	16	51	0	27	37	6
Annual_precip	43	64	22	100	60	45
Temp_range	82	43	65	97	18	100
Forested_2001	17	3	7	27	48	23
Agriculture_2001	66	33	31	55	35	23
Developed_2001	5	16	33	86	70	16
Open_water_2001	9	4	25	0	14	5
Wetland_2001	59	64	44	96	34	8
Delta_forested	6	13	1	37	4	0
Delta_agriculture	17	32	11	55	12	16
Delta_developed	0	24	93	29	17	41
Delta_open_water	11	0	55	72	8	16
Delta_wetland	11	8	36	89	27	1

Table 8. Random Forest (RF) results for flow timing by ecoregion, mtry = 4, trees = 5000, 10-fold cross-validation. Predictor values ≥ 70 are considered important. Red colors indicate negative relationships, and blue colors indicate positive relationships. Darker shading indicates importance = 100, medium shading indicates 100 > importance ≥ 70, lighter shading indicates importance < 70 but still among the top three. Gray shading indicates non-monotonic relationships.

	Timing					
	CP tl2	**PD tl2**	**MT tl2**	**CP ta2**	**PD ta2**	**MT ta2**
R^2	0.54	0.62	0.45	0.62	0.67	0.66
Drainage_area	0	20	19	100	100	100
Montane_PCA	25	23	16	86	62	23
Soil_cation	15	0	9	19	3	16
Dam	3	83	100	63	37	31
Annual_precip	66	58	38	46	38	26
Temp_range	100	66	16	81	17	39
Forested_2001	64	9	30	25	0	10
Agriculture_2001	16	20	93	36	4	0
Developed_2001	30	17	26	16	10	6
Open_water_2001	55	100	74	11	1	21
Wetland_2001	71	12	22	69	32	44
Delta_forested	27	2	0	16	9	12
Delta_agriculture	17	23	41	29	8	0
Delta_developed	8	15	34	17	21	24
Delta_open_water	10	27	12	30	10	8
Delta_wetland	16	14	10	0	9	18

Table 9. Random Forest (RF) results for flow duration by ecoregion, mtry = 4, trees = 5000, 10-fold cross-validation. Predictor values ≥ 70 are considered important. Red colors indicate negative relationships, and blue colors indicate positive relationships. Darker shading indicates importance = 100, medium shading indicates 100 > importance ≥ 70, lighter shading indicates importance < 70 but still among the top three. Gray shading indicates non-monotonic relationships.

	Duration					
	CP dl16	**PD dl16**	**MT dl16**	**CP dh15**	**PD dh15**	**MT dh15**
R^2	0.50	0.63	0.51	0.77	0.59	0.57
Drainage_area	100	19	26	100	5	1
Montane_PCA	61	71	20	42	23	29
Soil_cation	67	14	88	34	0	100
Dam	11	37	13	0	7	0
Annual_precip	0	52	48	23	26	69
Temp_range	23	60	100	50	13	99
Forested_2001	23	44	41	49	46	11
Agriculture_2001	26	100	20	14	49	16
Developed_2001	34	92	25	3	100	17
Open_water_2001	38	26	46	6	71	25
Wetland_2001	61	77	4	74	33	9
Delta_forested	29	26	50	14	11	37
Delta_agriculture	45	42	36	12	39	9
Delta_developed	21	59	45	1	33	33
Delta_open_water	16	6	37	10	33	35
Delta_wetland	18	0	0	4	32	7

Table 10. Random Forest (RF) results for rate-of-change by ecoregion, mtry = 4, trees = 5000, 10-fold cross-validation. Predictor values ≥ 70 are considered important. Red colors indicate negative relationships, and blue colors indicate positive relationships. Darker shading indicates importance = 100, medium shading indicates 100 > importance ≥ 70, lighter shading indicates importance < 70 but still among the top three. Gray shading indicates non-monotonic relationships.

	Rate-of-Change					
	CP ra1/ma2	**PD ra1/ma2**	**MT ra1/ma2**	**CP ra8**	**PD ra8**	**MT ra8**
R^2	0.31	0.61	0.64	0.64	0.50	0.56
Drainage_area	100	71	78	81	57	6
Montane_PCA	34	100	19	89	79	20
Soil_cation	39	2	37	44	0	100
Dam	61	57	0	3	83	30
Annual_precip	73	61	43	22	39	36
Temp_range	70	18	100	19	16	49
Forested_2001	19	46	31	33	69	29
Agriculture_2001	45	25	13	31	96	12
Developed_2001	60	62	18	28	100	15
Open_water_2001	55	15	9	18	42	62
Wetland_2001	48	36	23	100	100	6
Delta_forested	0	4	8	0	18	14
Delta_agriculture	50	0	16	28	33	2
Delta_developed	54	19	34	12	49	27
Delta_open_water	45	0	33	33	16	4
Delta_wetland	20	17	2	41	7	0

Table 11. Random Forest (RF) results by flow dimension, all ecoregions combined, mtry = 4, trees = 5000, 10-fold cross-validation. This table indicates proportion of models in which the predictor had an importance score of ≥ 70. Proportions are scaled by color from 0.33 to 0.67.

Variable	Magnitude	Frequency	Duration	Timing	Rate-of-change
Drainage_area	0.67	0.50	0.33	0.50	0.67
Montane_PCA	0.17	0.50	0.17	0.17	0.50
Soil_cation	0.00	0.00	0.33	0.00	0.17
Dam	0.00	0.00	0.00	0.33	0.17
Annual_precip	0.17	0.17	0.00	0.00	0.17
Temp_range	0.33	0.50	0.33	0.33	0.33
Forested_2001	0.00	0.00	0.00	0.00	0.00
Agriculture_2001	0.00	0.00	0.17	0.17	0.17
Developed_2001	0.00	0.17	0.33	0.00	0.17
Open_water_2001	0.00	0.00	0.17	0.33	0.00
Wetland_2001	0.00	0.17	0.33	0.17	0.33
Delta_forested	0.00	0.00	0.00	0.00	0.00
Delta_agriculture	0.00	0.00	0.00	0.00	0.00
Delta_developed	0.00	0.17	0.00	0.00	0.00
Delta_open_water	0.00	0.17	0.00	0.00	0.00
Delta_wetland	0.00	0.17	0.00	0.00	0.00

Table 12. Random Forest (RF) results by ecoregion, all flow dimensions combined, mtry = 4, trees = 5000, 10-fold cross-validation. This table indicates the proportion of models in which the predictor had an importance score ≥ 70. Proportions are scaled by color from 0.30 to 0.70.

Variable	CP	PD	MT	Average
Drainage_area	0.70	0.50	0.40	0.53
Montane_PCA	0.30	0.60	0.00	0.30
Soil_cation	0.00	0.00	0.30	0.10
Dam	0.00	0.20	0.10	0.10
Annual_precip	0.20	0.10	0.00	0.10
Temp_range	0.60	0.00	0.50	0.37
Forested_2001	0.00	0.00	0.00	0.00
Agriculture_2001	0.00	0.20	0.10	0.10
Developed_2001	0.10	0.30	0.00	0.13
Open_water_2001	0.00	0.20	0.10	0.10
Wetland_2001	0.40	0.20	0.00	0.20
Delta_forested	0.00	0.00	0.00	0.00
Delta_agriculture	0.00	0.00	0.00	0.00
Delta_developed	0.00	0.00	0.10	0.03
Delta_open_water	0.10	0.00	0.00	0.03
Delta_wetland	0.10	0.00	0.00	0.03

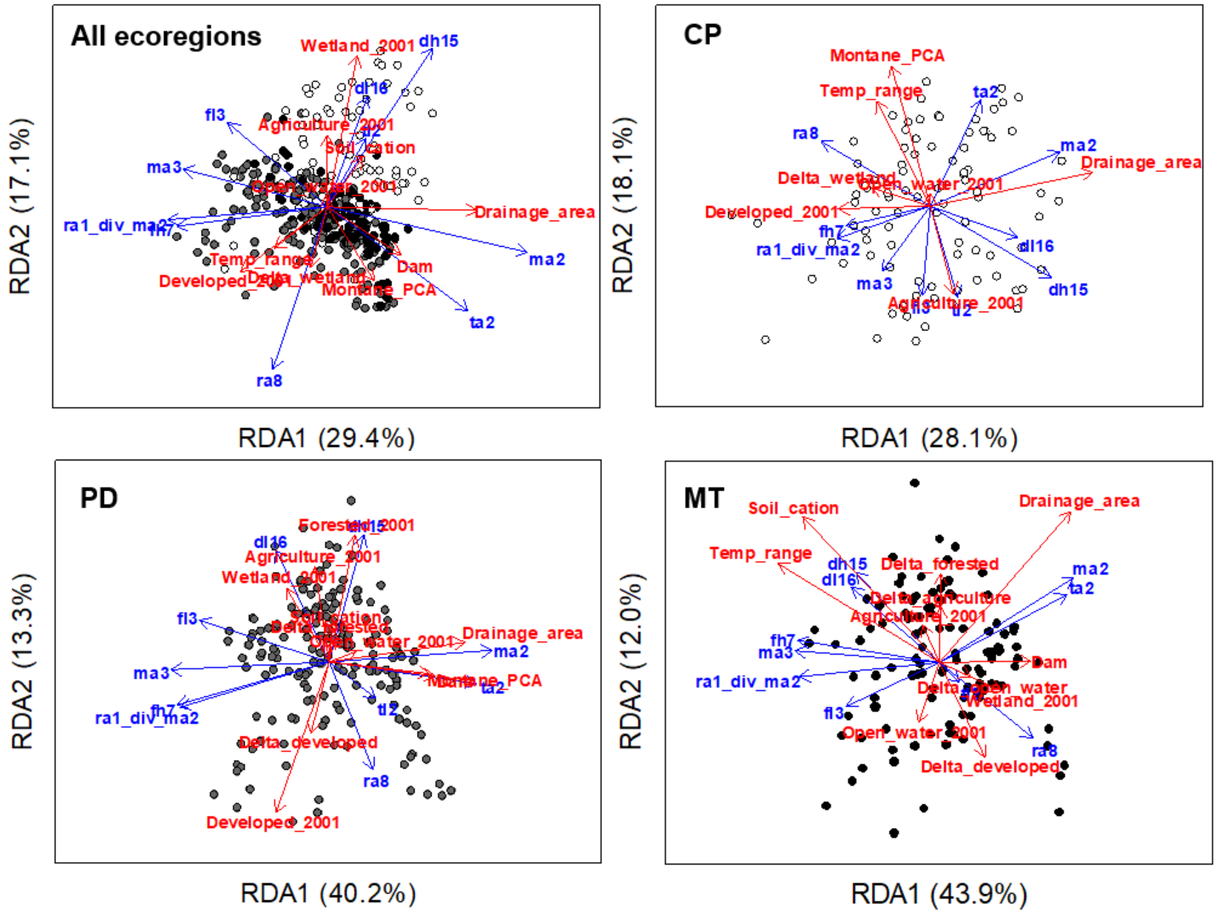

Figure 2. Ordinations based on redundancy analyses, seeking to explain variation in 10 hydrologic indices (blue vectors) based on candidate environmental predictor variables (red vectors). The top left panel is based on an analysis including all sites.

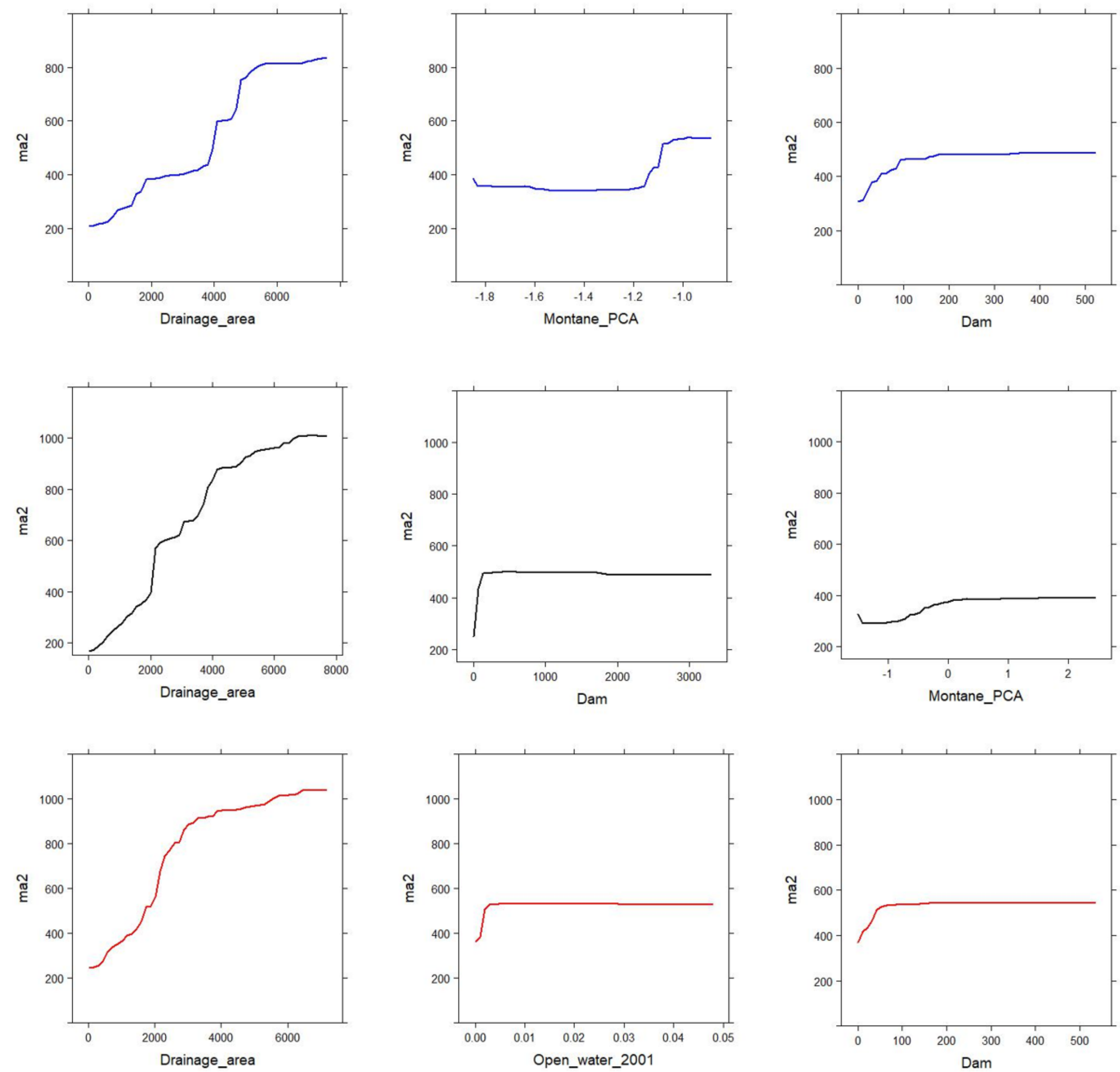

Figure 3. PDP Plots for the top three most important environmental variables for ma2 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

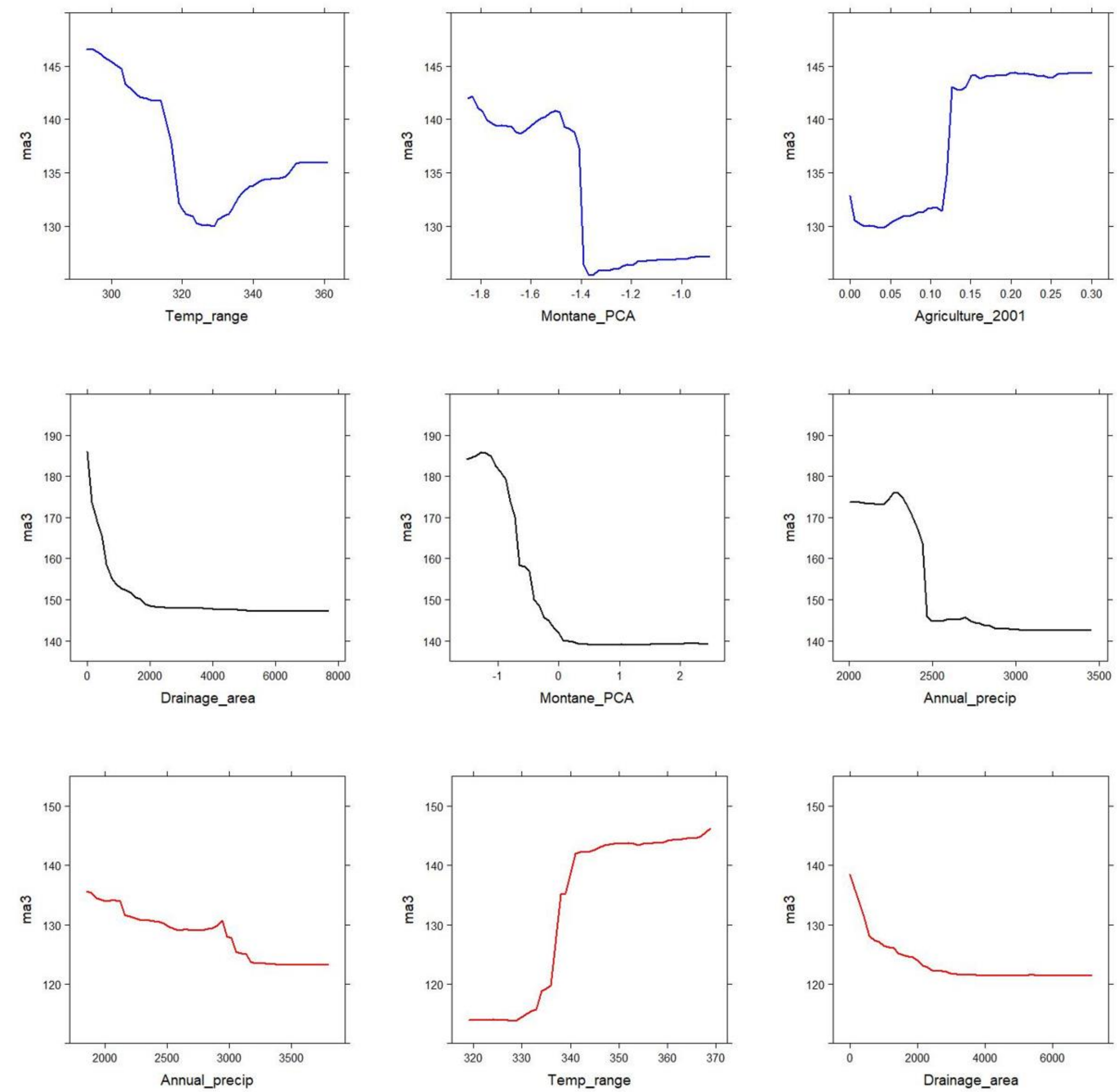

Figure 4. PDP Plots for the top three most important environmental variables for ma3 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

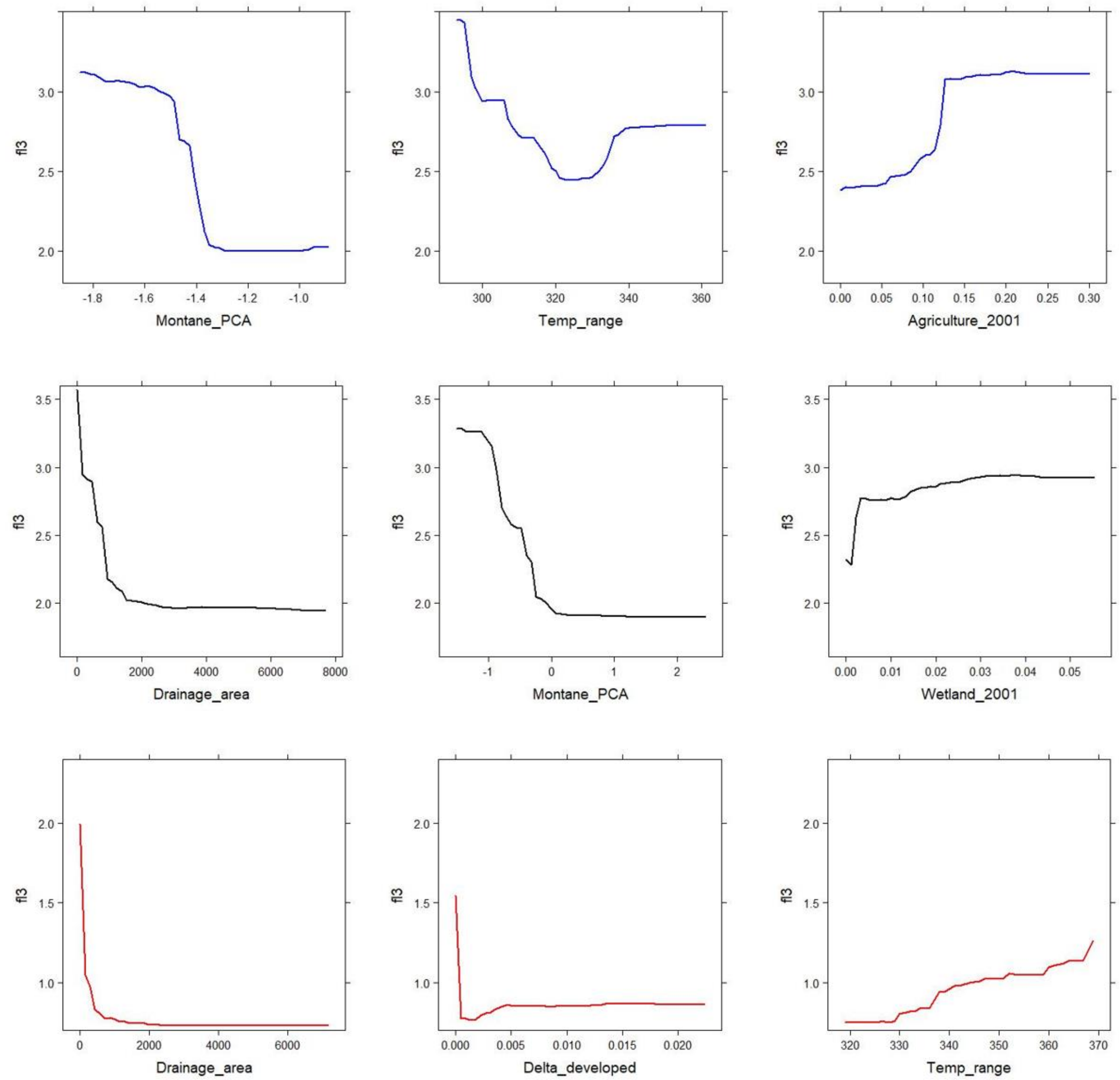

Figure 5. PDP Plots for the top three most important environmental variables for fl3 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

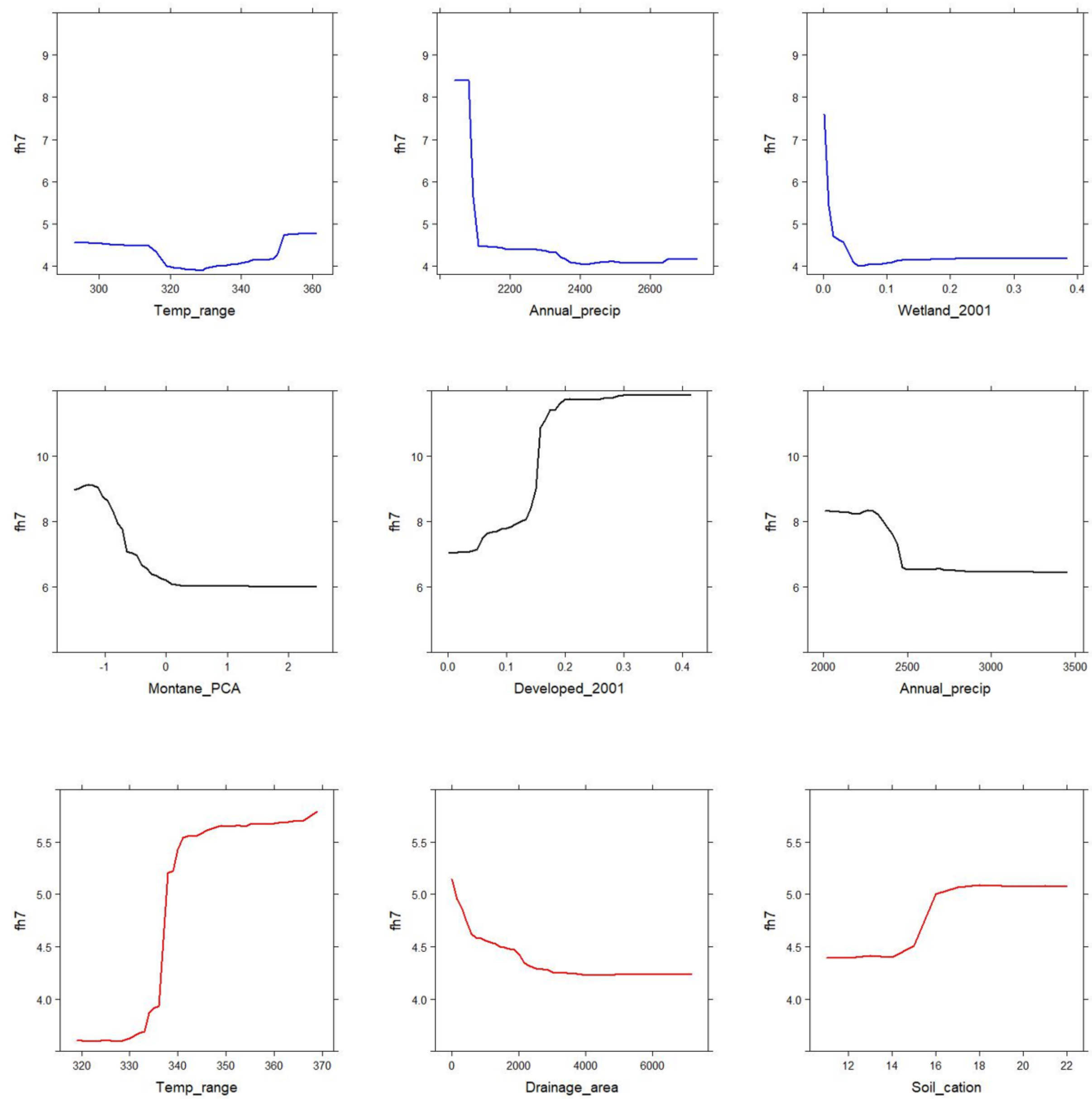

Figure 6. PDP Plots for the top three most important environmental variables for fh7 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

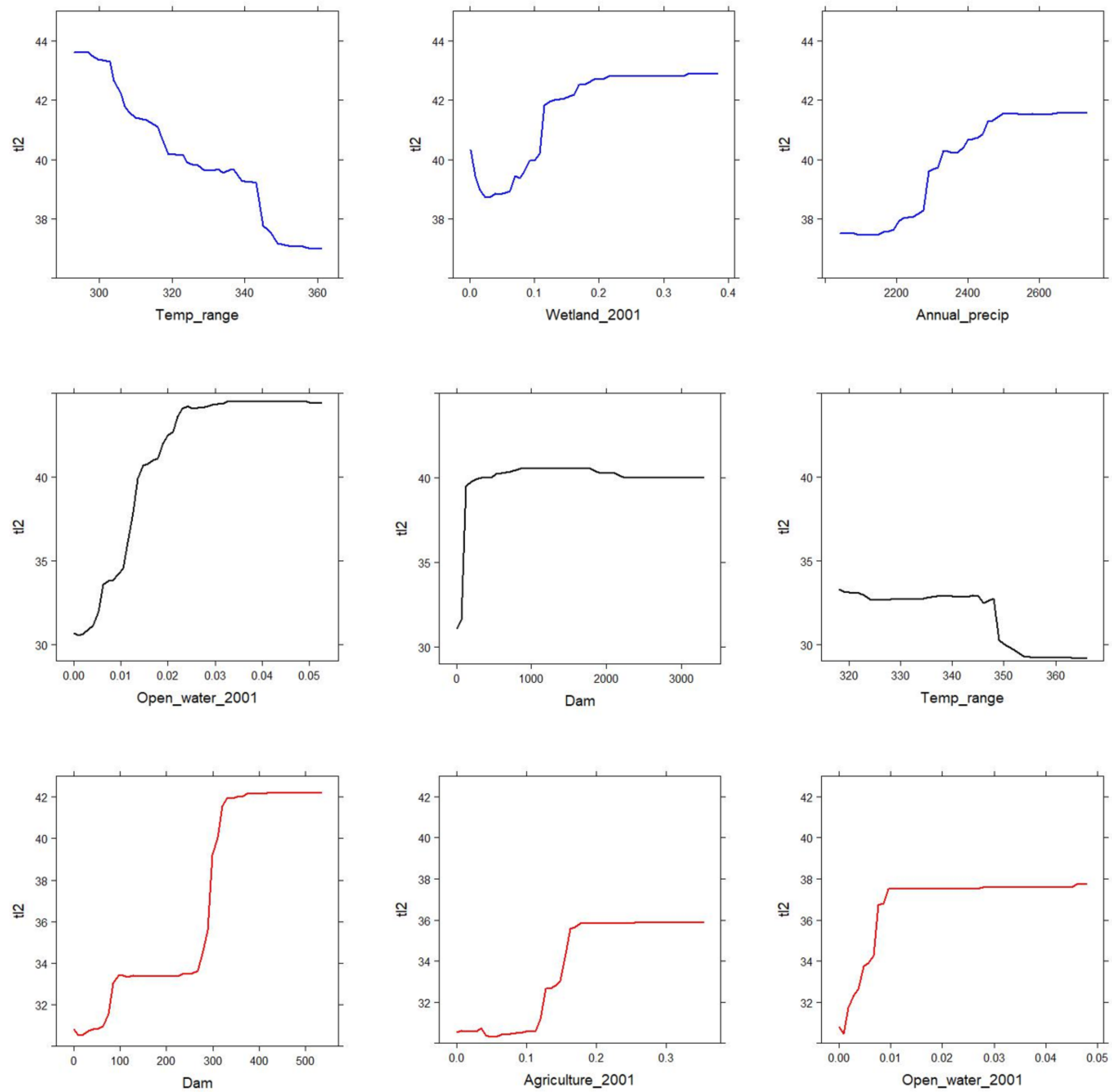

Figure 7. PDP Plots for the top three most important environmental variables for tl2 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

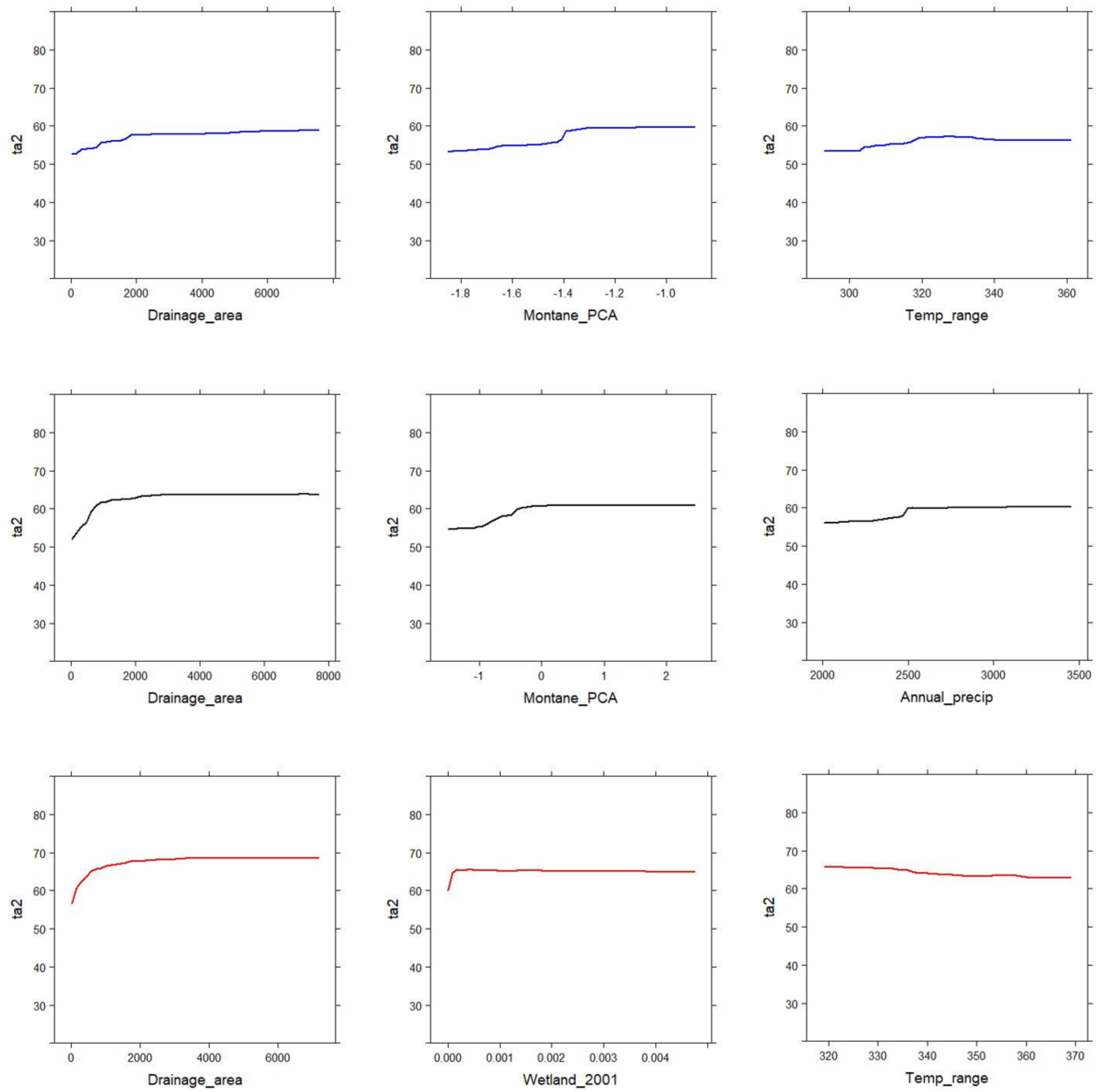

Figure 8. PDP Plots for the top three most important environmental variables for ta2 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

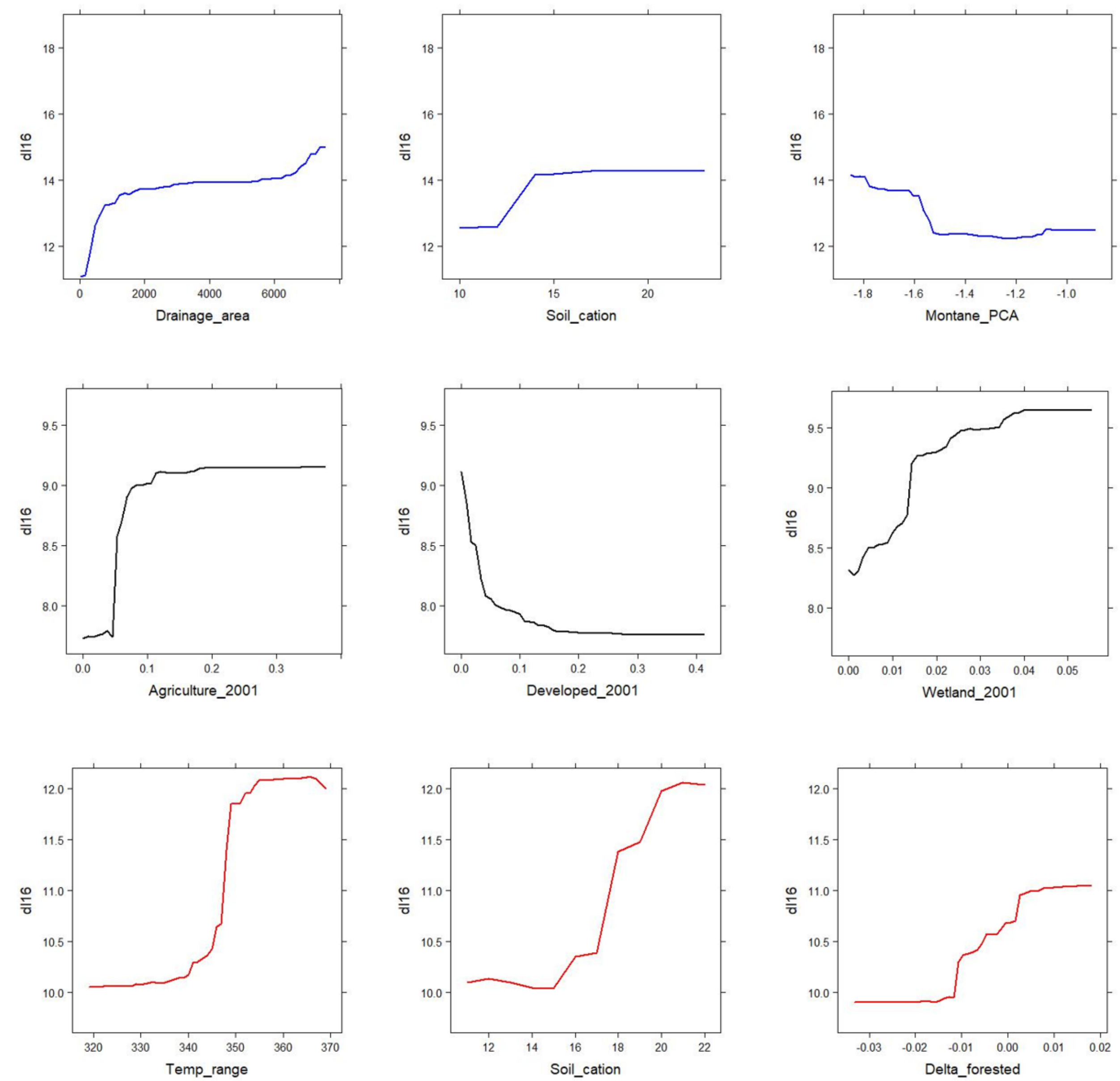

Figure 9. PDP Plots for the top three most important environmental variables for dl16 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

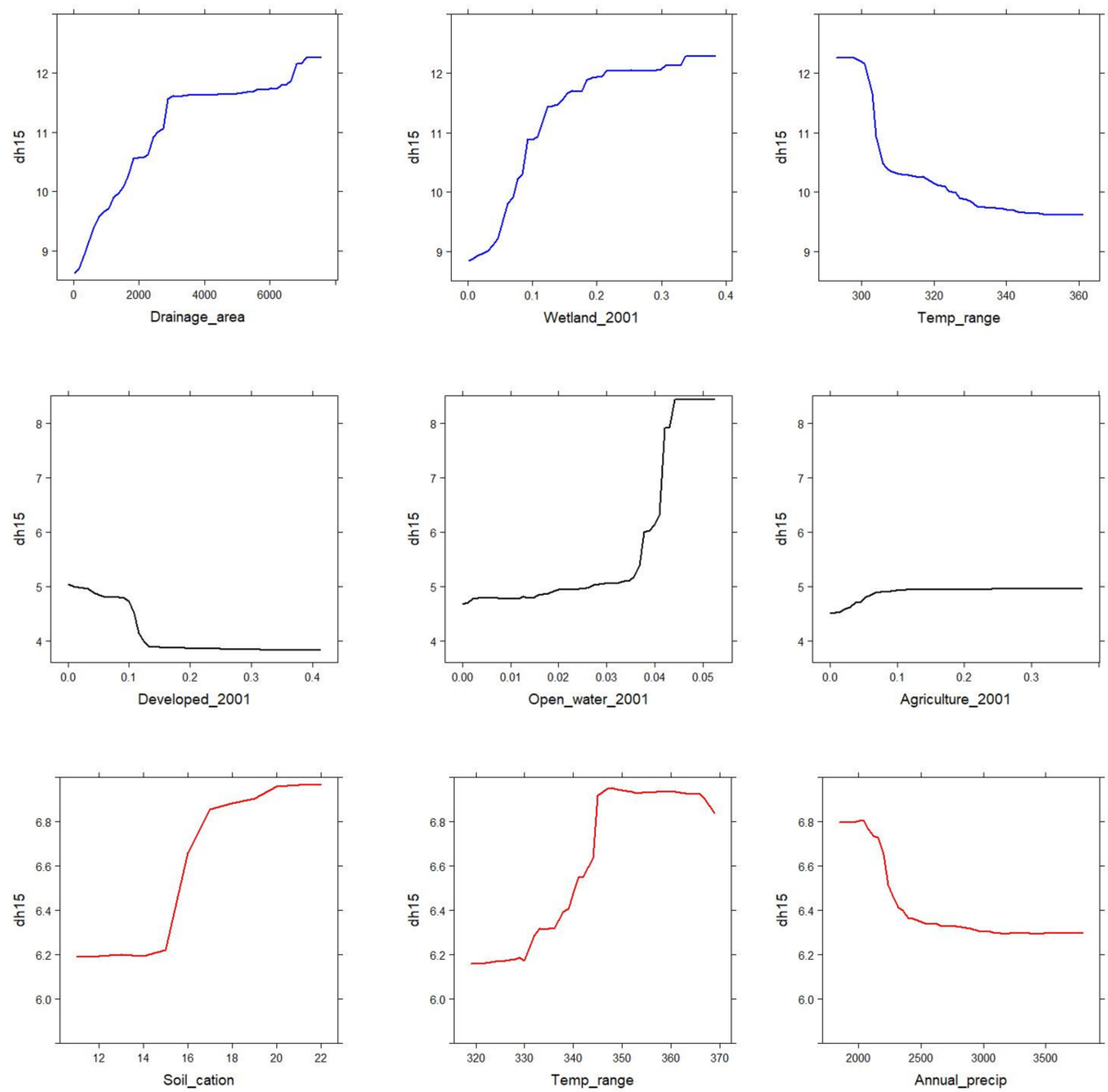

Figure 10. PDP Plots for the top three most important environmental variables for dh15 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

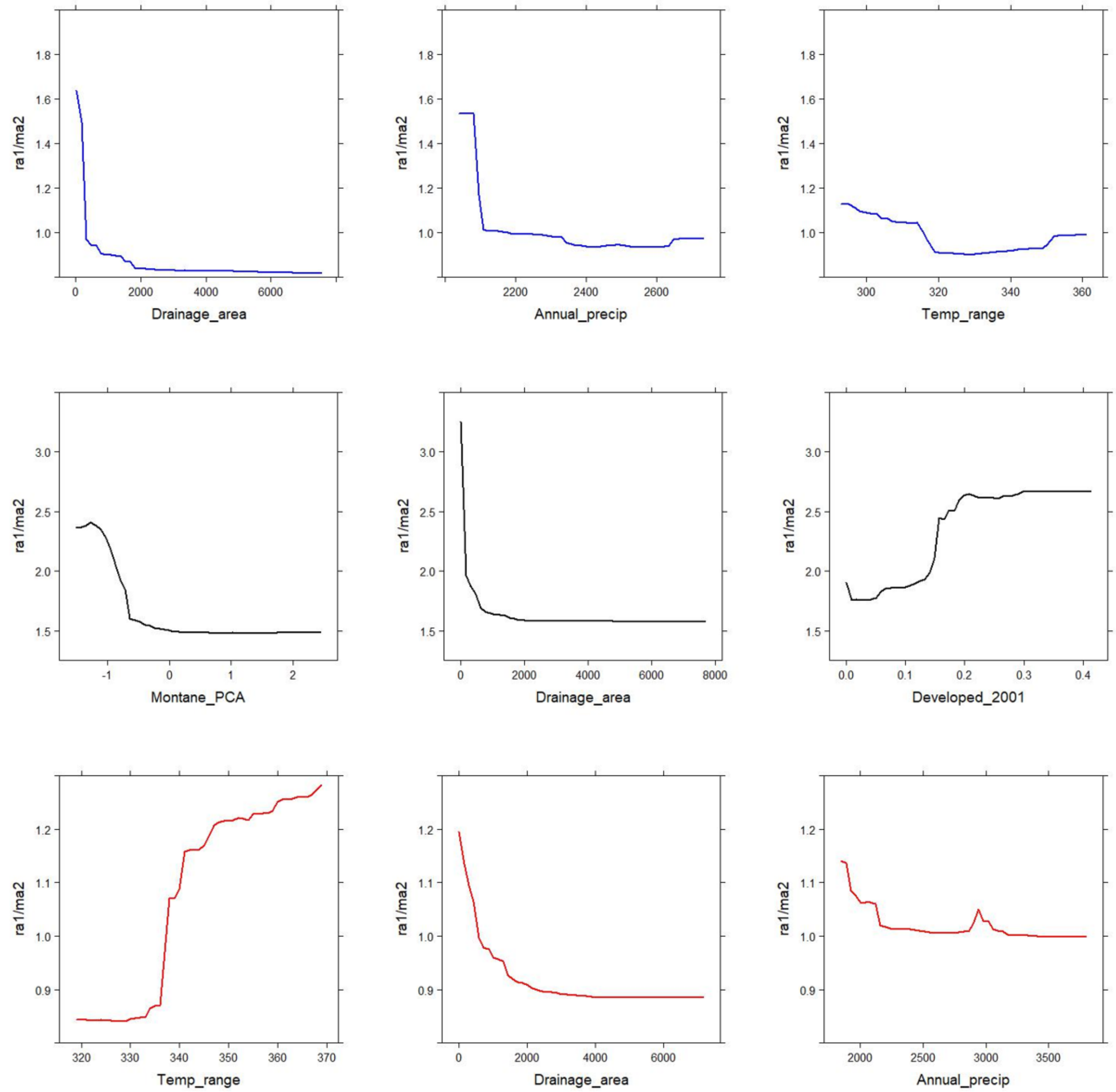

Figure 11. PDP Plots for the top three most important environmental variables for ra1/ma2 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

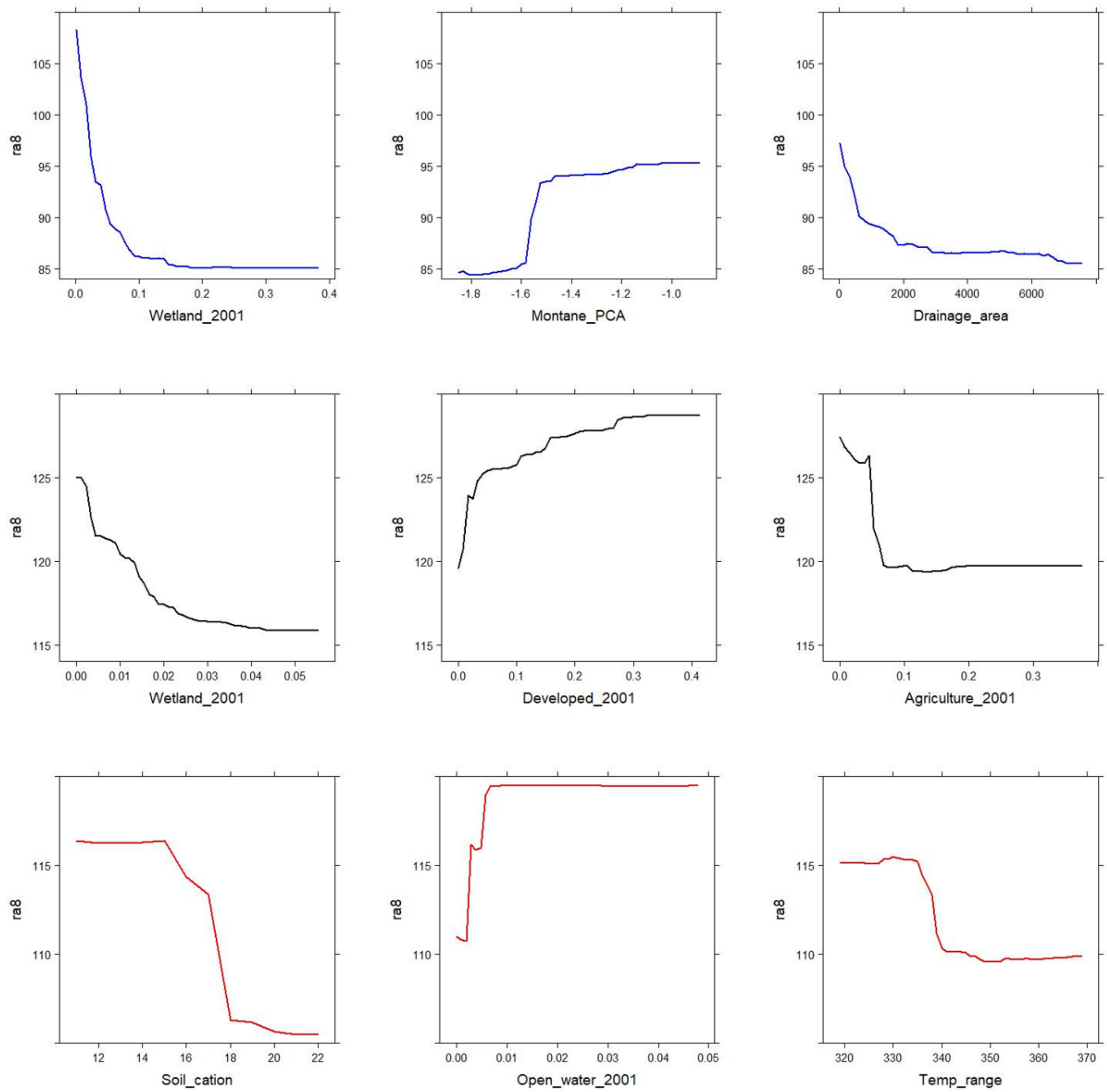

Figure 12. PDP Plots for the top three most important environmental variables for ra8 by ecoregion. The top row represents CP (blue), the middle row represents PD (black), and the bottom row represents MT (red). Variables are listed in the order of importance from left to right.

CHAPTER 4

DISCUSSION

Variation of Flow Regimes Among Ecoregions

Prior to beginning this study, I predicted that ecoregional flow regimes would "sort out" into distinct groups: upland and lowland, with PD streams exhibiting flow regimes intermediate to these two other groups. I presumed from the MT to the CP, there would be gradients in flashiness, frequency of high and low flows, and duration associated with clear environmental gradients (elevation, topography, climate). Though PD and MT flow regimes exhibited some overlap in the "All ecoregions" RDA model, PD streams were not intermediate along a gradient between upland and lowland groupings. This result could be due to the confounding and large influences on urbanization and flow regulation on PD streams. Smock and Gilinsky (1992) and Marion et al. (2015) both describe the unique differences between CP streams compared to those of other ecoregions (channel material, topography, access to groundwater, extreme weather, increased flow regime variation). On the other end of the topographic spectrum, MT streams are known for their high gradient, presence of bedrock control, strong variation in seasonal discharge, and increased geologic impacts (Wohl 2000). While PD streams bordering MT and CP ecoregions do tend to share overlapping features, I underestimated the impacts of development in PD watersheds and wetland cover in CP watersheds. Almost 20% of the CP landscape was dominated by wetland and was a differentiating factor in hydrology compared to the other two groups (Table 1). Extensive development in PD watersheds is directly related to flashiness and altered flow frequency (Schoonover et al. 2006). Though the Piedmont and Southern Coastal Plain level III ecoregions share similar developed land cover percentages, CP models indicated weak association between development and flow regimes, unlike PD models.

I found ecoregional flow regimes to be unique from one another and largely characterized by different dimensions of flow. CP flow regimes were characterized by longer high and low duration flow events that were less flashy than other groups. Naiman et al. (2005) explains that larger streams are often less flashy in response to precipitation events compared to small streams higher in the watershed, and CP stream gage locations had larger watershed areas on average compared to the other two ecoregional groups. According to Marion et al. (2015), lowland stream ecosystems are often associated with pronounced variation in seasonal flow regimes, and the longer high and low duration CP flow events indicated by RDA results aligns with this sentiment. PD streams had increased CV of daily flows, more frequent high flows, and increased flow rise rates. Piedmont stream association with development in this study aligns with the findings of Paul and Meyer (2001) and Walsh et al. (2005), urbanization leads to increased high flows during storm events, and decreased rates of baseflow, leading to greater daily flow variability. MT streams were more predictable with higher average magnitudes, more frequent high flows, and increased flow rise rates. Poff et al. (2007) describes the homogenizing impact of dams on associated flow regimes. The results of this study potentially corroborate those findings, as many dams (especially hydroelectric) reduce variability in daily flows due to timed releases (Poff et al. 2010, Ruhi et al. 2018, Zhang et al. 2018). Additional investigation into causality based on the results of this study would be warranted.

Environmental Drivers of Flow Variation

A small group of environmental factors stood out among the rest in terms of influence. Drainage area, topography, and upstream temperature range tended to be among the most important predictors of flow regardless of flow dimension or ecoregion. I hypothesized that drainage area would be an important predictor variable, and analyses confirmed that drainage area was the most important predictor of flows across ecoregions and flow dimensions. It is well known that smaller streams tend to be flashier, more intermittent, and more responsive to small rain events, and larger streams have greater flood magnitudes, are generally less flashy, more predictable, and exhibit longer flow durations (Scott et al. 2019, Royall 2021). The overall importance of the stream size (Drainage_area) variable suggests a meaningful gradient of stream sizes has been captured in the study area. Further, by statistically accounting for the influence of stream size, I was able to look past the large impact of stream size and see how other factors influence hydrology, all while holding stream size constant. It is worth noting that stream size was not always a top predictor. Topography was a more important predictor across all PD models, and upstream temperature range was a more important predictor across all MT models.

Random forest and RDA results were generally aligned, but in the instance of CP hydrology and wetlands, results conflicted between the two modeling methods. Interestingly, wetland cover distinguished CP streams from other groupings in the global model, but wetland cover was found to be an insignificant variable during stepwise variable selection for modeling of CP streams alone. Instead, stream size, topography, as well as agricultural and developed land cover distinguished CP streams from one another. This suggests that wetlands are so common in CP systems that their consideration is not helpful for distinguishing one CP stream from another. Tiner (2003) suggests that even weak wetland surface connections can play an important role in determining the hydrology of landscapes. MT and PD watersheds are comprised of less than 1% wetland, compared to CP streams where watersheds are close to 20% wetland (Table 1). The random forest summary by ecoregion indicated that wetlands are a top three predictor of hydrology across all CP models, unlike RDA which deemed the variable insignificant. It is possible that wetlands were obscured by another variable in the CP RDA such as change in wetland cover, as the Delta_wetland variable was only found to be significant in the global model and CP model (APPENDIX III).

I hypothesized that agricultural cover would be a driver of flashiness across all ecoregions, but that was not the case with PD streams. In PD streams, flashiness increased with development, and decreased as forested cover, agricultural cover, and wetland cover increased, indicating this ecoregional group was largely characterized by land cover. The negative relationship between agriculture and flashiness could possibly be due to agricultural cover not being completely impervious to infiltration. In reference to flashiness increasing due to development, Russell et al. (2017) explains that across 21 studies comparing urban and agricultural watersheds, urban streams moved three times the amount of annual suspended sediment, indicating that developed cover leads to flashier, more erodible systems. Multiple studies have found that stream degradation begins to take place when the watershed reaches approximately 10% impervious cover (Bledsoe and Watson 2001, Wang et al. 2001, Jennings and Taylor

Jarnagin, 2002). Schoonover et al. (2006) found that pastoral watersheds were less flashy than urbanized watersheds. The agricultural variables in this study were a combination of pasture/hay cover and cultivated crop cover. Separating these variables could have led to different results, as pastures have increased surface protection compared to cultivated crop cover (Yimer et al. 2008, Panagos 2015).

Mountain flow regimes were uniquely related to soil cation exchange capacity (CEC). Increased CEC is associated with increased clay content, pH, and organic matter (Kissel et al. 2008). Soil cation exchange capacity is generally used by soil scientists to measure fertility for crops, but the Soil Test Handbook for GA groups soils and associated CEC averages based on ecoregions (Kissel and Sonon 2008). CEC was included as an environmental variable in hopes to capture geologic impacts on flow regimes across ecoregions. MT streams with increased CEC were generally less flashy. It is possible that increased erosion in flashy watersheds is reducing soil fertility. Kurothe (2014) explains that increased runoff is directly related to soil fertility decline. Another reason for this relationship could be flashier streams tend to deposit more alluvial material in their associated watersheds. Kissel et al. (2008) discusses how alluvial mountain systems have sandier topsoil with clay beneath, and sandier soils have lower CEC values. Flashier low order streams in developed areas could be contributing to lower soil CEC. Schön (2011) elaborates on the increased clay content associated with sedimentary rock compared to igneous or metamorphic rock. It is also possible that CEC is capturing a response to the sedimentary nature of the level III Ridge and Valley ecoregion compared to the metamorphic and igneous nature of the level III Blue Ridge ecoregion.

Topography is directly related to stream geomorphology, and it is logically important considering upland ecoregions are being compared with lowland ecoregions. Topography was an important driver of ecoregional regimes in CP stream and PD streams across all modeling methodologies. Also, topography was an important predictor of flow frequency and rate-of-change. Interestingly, topography was not an important predictor of flow regimes in MT streams (consistent across RDA and RF models). Since MT streams are already associated with steeper terrain, it is likely that topography is not a differentiating factor. The MT streams in this study had an average watershed slope of 3.6 percent, meaning most streams had lower entrenchment ratios. Lowland streams with < 2% slope have greater floodplain access and true riffle-pool sequences, whereas streams with slope > 2% typically are less sinuous and exhibit step-pool features (Rosgen 1994). Similar step-pool bedform diversity and entrenchment ratios among MT streams likely explain why topography wasn't important in within-ecoregion models. More variation in bedform diversity, slope, and entrenchment ratios in PD and MT streams may explain the increased importance of topography in those regions.

The results of this study affirm the importance of considering anthropogenic drivers of flow when analyzing regional flow patterns. The importance of dams in RF and RDA models indicated that anthropogenic impacts are an established part of current flow regimes. Dams were an important predictor in 33% of all RF models related to timing and were associated with increased predictability in PD streams (global RDA model). Variable ra8 (an indicator of hydrologic alteration) highlighted the impact of dams on flow regimes in the PD (Richter et al. 1996, Olden and Poff 2003). Like flow regulation, climate change is also impacting ecosystems and natural regimes. Climate change alters the frequency and duration of low flows and reduces average flow magnitudes (Arthington 2012). Upstream air temperature range was an important predictor of all dimensions of flow, and was an important predictor of ecoregional flow regimes in the CP and MT. Air temperature is directly related to water temperature, infiltration rates of water in the stream bed, the water cycle, seasonal temperature changes, and evapotranspiration rates (Rorabough 1963, Yang et al. 2011). Air temperature can effectively shape flow regimes, and with this in mind, climate change will continue to become an increasingly important contributor to flows, especially when combined with other anthropogenic pressures such as dams and water abstraction (Schneider et al. 2013). The alteration of natural flow regimes has a positive impact on the chemical and physical processes of riverine systems, and just like the impact of dams, we should continue to expect further shifts away from natural flow conditions (Poff et al. 1997, Bunn and Arthington 2002)

Although RDA and RF models generally explained a substantial proportion of the variation in flow characteristics, unexplained variation may be due to the influence of a few key factors I was unable to index for this study. One example would be water abstraction. It would likely explain additional variation as it is considered one of the most important causes of flow regime alteration in river systems (Poff and Zimmerman 2010). Water abstraction has an obvious impact on flow regimes as it alters the availability of water, and directly impacts each dimension of flow. Hydropower, domestic/industrial use, and agricultural use are three relevant examples. Hydropower and domestic/industrial uses are more documented compared to agricultural use since states and municipalities have the power to set their own regulations and limits (or not set any). For example, in the state of Georgia, a permit is not required for water withdrawal under 100,000 gallons per day on a monthly average, and no permit is required to initially fill a farm pond (O.C.G.A. 12-5-31, 2010). Water abstraction data is not readily available from state to state, and water withdrawals deemed “small” and unworthy of a permit likely are import drivers of flow regimes that would be nearly impossible to track across a study area that spans four state boundaries. Another independent variable that would explain additional variation would be local stream geomorphology. Flow regimes are impacted by the geomorphology of the system, especially when considering stream stability. Streams with a low entrenchment ratio and a low sinuosity will exhibit increased flow velocities compared to more stable stream types (Rosgen 1994). The dominant stream type (a measure of stability) at each USGS gage was not captured in this study. USGS gages are typically located on bridges and overpasses, and these locations do not always exhibit natural geomorphic patterns. A geomorphic stream survey at each of the 375 USGS gages in the study area would require years of field effort and extensive travel. Some of the gages in question are in non-wadable streams that would require extensive LiDAR or ultrasonic surveying.

For flow relationships summarized by dimension or ecoregional group, I found that dimensions of flow were not equally associated with every environmental predictor. This was also the case for within-dimension metrics (ex. ma2 vs. ma3). Duration, timing, and rate-of-change metrics were more sensitive to anthropogenic impacts and land cover compared to magnitude and frequency metrics. Additionally, there were no examples where environmental predictors had the same importance ranking for two indices associated with the same flow dimension. For example, in CP streams, wetland cover was the most important predictor of flow direction change (ra8) but was unimportant in reference to rise rate within the same ecoregion, even though both indices are a measure of rate-of-change. The results of this study have indicated that asking specific questions about the relationship between a particular environmental predictor and an entire dimension of flow is only an initial step. Questions about relationships between flow and the environment must be focused on a particular element of a given dimension.

Applications of This Study

Based on results of this study, relationships between flow regimes and environmental factors often do not transfer well across ecoregional boundaries. Anthropogenic impacts were more important in determining flow regimes of PD streams compared to MT or CP. Duration, timing, and rate-of-change were more sensitive than magnitude and frequency to flow regulation and urban development, whereas magnitude and frequency are more often the primary focus of flow regulations for dams (Poff et al. 2010, Zhang et al. 2018, Ruhi et al. 2018). At a regional level, biotic community compositions (or assemblages) are influenced by zoographic ecoregional breaks, land cover change, and watershed area (Ricklefs 1987, Jackson and Harvey 1989, Angermeier and Winston 1998, Hoeinghaus et al. 2007). Additionally, organisms have developed foraging strategies and evolved physiologically based on associated flow regimes (Poff and Allen 1995, Poff et al. 1997, Bunn and Arthington 2002). The impacts of altering flow regimes is not isolated to a specific taxonomic group. Alteration of flow regime components (magnitude, frequency, timing, duration, and rate-of-change) can change macroinvertebrate, fish, and amphibian assemblage structures, in turn, causing community instability and alteration of food webs (Baron et al. 2002).

Hydrologic regimes are a major constraint on biota, and patterns in the flow regime often directly affect the structure of local biotic communities (Fausch and Bramblett 1991). This makes sense considering hydrologic extremes place constraints on biotic assemblages, and assemblages evolve based on those flow constraints (Poff 1992). Ecoregional groups like the PD, with important anthropogenic drivers of flow, are at risk of losing aquatic biodiversity due to drastic changes in flow regimes over a short span of ecological time. Mims and Olden (2013) found that dams alter the composition of communities by favoring equilibrium strategists and disfavoring opportunists. The results of this study indicated dams were an important predictor of flow timing and have a greater impact on PD streams than CP streams. A summary of literature examining flow-fish relationships found altered timing (due to hydropower) impacted fish biomass, abundance, diversity, and community structure (Rytwinski et al. 2020). Overall, organisms that have evolved in association with natural flow regimes will likely not be able to respond to new anthropogenic drivers of flow in time, leading to declines in richness, and only the persistence of more tolerant organisms and life histories.

With this in mind, my results reinforce the importance of tailored approaches to restoration and protection efforts. Protecting sensitive native species in freshwater lotic systems means tuning our conservation efforts to a specific ecoregion or watershed. Many imperiled species require hydrologic management where flows must be regulated to meet specific flow-related life history requirements, and an improved understanding of ecoregional flow relationships would increase the likelihood of successful recovery efforts. These results could help improve management decisions, in turn improving species diversity, fisheries productivity, and persistence of imperiled species.

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APPENDIX I

Original NLCD Land Cover classes that were grouped and renamed based on year and variable type. Column "New ID (2001)" refers to variables that were grouped based on data from the year 2001. Column "New ID (Delta)" refers to variables that were grouped based on the change in land cover from the year 2001 to 2016.

NLCD #	**NLCD Land Cover Class**	**New ID (2001)**	**New ID (Delta)**
11	Open Water	Open_Water_2001	Delta_open_water
22	Developed, Low Intensity	Developed_2001	Delta_developed
23	Developed, Medium Intensity	Developed_2001	Delta_developed
24	Developed, High Intensity	Developed_2001	Delta_developed
41	Deciduous Forest	Forested_2001	Delta_forested
42	Evergreen Forest	Forested_2001	Delta_forested
43	Mixed Forest	Forested_2001	Delta_forested
81	Pasture/Hay	Agriculture_2001	Delta_agriculture
82	Cultivated Crops	Agriculture_2001	Delta_agriculture
90	Woody Wetlands	Wetland_2001	Delta_wetland
95	Emergent Herbaceous Wetlands	Wetland_2001	Delta_wetland

APPENDIX II

Correlation matrix of environmental predictor variables.

	Dam	Drainage_area	Montane_PCA	Temp_range	Annual_precip	Soil_cation	Open_water_2001	Developed_2001	Forested_2001	Agriculture_2001	Wetland_2001	Delta_open_water	Delta_developed	Delta_forested	Delta_agriculture
Dam															
Drainage_area	0.27														
Montane_PCA	-0.08	-0.16													
Temp_range	-0.03	-0.15	0.14												
Annual_precip	0.03	-0.02	0.37	-0.56											
Soil_cation	-0.11	-0.05	0.48	0.32	-0.26										
Open_water_2001	0.32	0.15	-0.20	-0.09	0.01	-0.24									
Developed_2001	-0.02	-0.10	-0.17	-0.08	-0.08	-0.24	0.00								
Forested_2001	-0.05	-0.20	0.53	0.23	0.34	0.06	-0.03	-0.44							
Agriculture_2001	-0.06	0.09	-0.34	0.06	-0.32	0.08	-0.02	-0.23	-0.24						
Wetland_2001	-0.06	0.13	-0.47	-0.51	-0.01	0.02	0.00	-0.11	-0.41	0.22					
Delta_open_water	0.04	0.05	-0.11	-0.10	0.04	-0.13	0.04	-0.07	0.01	0.08	0.06				
Delta_developed	0.03	-0.02	-0.15	-0.16	0.05	-0.28	0.11	0.58	-0.27	-0.08	-0.08	-0.05			
Delta_forested	0.00	-0.01	0.28	0.04	0.14	0.22	-0.11	-0.24	0.14	-0.03	-0.12	0.01	-0.54		
Delta_agriculture	-0.03	0.01	0.20	0.05	0.06	0.31	-0.09	-0.20	0.10	-0.29	0.17	-0.14	-0.65	0.38	
Delta_wetland	-0.05	-0.12	0.22	0.21	0.03	0.15	-0.16	-0.07	0.25	-0.04	-0.29	-0.26	-0.22	0.11	0.08

APPENDIX III

Results of stepwise model selection for RDA input (p-in=0.05, p-out=0.05); blanks indicate non-significant variables.

Environmental Variable	All ecoregions			Coastal Plain		
	Variance	F	P	Variance	F	P
Drainage_area	0.907	72.143	0.001	1.719	31.520	0.001
Developed_2001	0.352	27.963	0.001	0.320	5.876	0.002
Temp_range	0.096	7.607	0.001	0.815	14.952	0.001
Montane_PCA	0.244	19.421	0.001	0.956	17.536	0.001
Wetland_2001	0.212	16.848	0.001			
Agriculture_2001	0.053	4.241	0.009	0.396	7.255	0.001
Dam	0.076	6.075	0.001			
Soil_cation	0.158	12.568	0.001			
Delta_developed						
Forested_2001						
Delta_wetland	0.063	5.000	0.003	0.240	4.402	0.005
Open_water_2001	0.173	13.766	0.001	0.204	3.741	0.019
Delta_forested						
Delta_agriculture						
Delta_open_water						
Annual_precip						

APPENDIX III CONTINUED

Remaining results of stepwise model selection for RDA input (p-in=0.05, p-out=0.05); blanks indicate non-significant variables.

Environmental Variable	Piedmont			Mountains		
	Variance	F	P	Variance	F	P
Drainage_area	0.7708	33.5287	0.001	1.045	28.761	0.001
Developed_2001	0.2295	9.9827	0.001			
Temp_range				0.665	18.299	0.001
Montane_PCA	0.9332	40.5955	0.001			
Wetland_2001	0.2036	8.8564	0.001	0.196	5.406	0.005
Agriculture_2001	0.1593	6.9286	0.001	0.270	7.425	0.001
Dam	0.0916	3.9838	0.011	0.112	3.095	0.034
Soil_cation	0.0566	2.4603	0.058	0.231	6.355	0.001
Delta_developed	0.0925	4.0234	0.013	0.254	6.994	0.001
Forested_2001	0.0755	3.2856	0.031			
Delta_wetland						
Open_water_2001	0.3291	14.3179	0.001	0.100	2.765	0.055
Delta_forested	0.2011	8.7471	0.001	0.151	4.168	0.012
Delta_agriculture				0.148	4.081	0.013
Delta_open_water				0.145	3.989	0.008
Annual_precip						

APPENDIX IV

RDA results for all two of the four models. Columns show the loadings for environmental and hydrologic variables for the first two loadings. Variables with missing values were deemed insignificant variables during stepwise variable selection and were not included in the associated model.

Variables	**All Ecoregions**		**CP**	
	RDA1	**RDA2**	**RDA1**	**RDA2**
Drainage_area	0.8454	-0.0216	0.8914	0.1853
Wetland_2001	0.1686	0.8459		
Montane_PCA	0.2634	-0.4139	-0.2088	0.7688
Soil_cation	0.2004	0.2751		
Developed_2001	-0.4881	-0.3631	-0.5015	-0.0149
Open_water_2001	-0.0052	0.0617	0.0049	0.0676
Temp_range	-0.2965	-0.2360	-0.2899	0.5739
Dam	0.4168	-0.2700		
Delta_wetland	-0.0891	-0.3403	-0.3182	0.0969
Agriculture_2001	0.0030	0.3996	0.1321	-0.4813
Forested_2001				
Delta_developed				
Delta_forested				
Delta_agriculture				
Delta_open_water				
Annual_precip				
ma2	2.1513	-0.4890	1.3939	0.5843
ma3	-1.5441	0.4045	-0.5168	-0.7037
fl3	-1.0665	0.9090	-0.0840	-0.9630
fh7	-1.6173	-0.2091	-0.9089	-0.2160
dl16	0.4328	1.1881	0.9451	-0.3356
dh15	1.1326	1.7034	1.2962	-0.7698
ta2	1.5180	-1.1218	0.5526	1.1370
tl2	0.4223	0.7387	0.3032	-0.9848
ra1_div_ma2	-1.7185	-0.1450	-0.9987	-0.3494
ra8	-0.5754	-1.7482	-1.1710	0.6995
Variance Explained	29.4%	17.1%	28.1%	18.1%

APPENDIX IV CONTINUED

RDA results for the last two models. Columns show the loadings for environmental and hydrologic variables for the first two loadings. Variables with missing values were deemed insignificant variables during stepwise variable selection and were not included in the associated model.

Variables	**PD**		**MT**	
	RDA1	**RDA2**	**RDA1**	**RDA2**
Drainage_area	0.7734	0.1123	0.5735	0.6549
Wetland_2001	-0.2440	0.4195	0.2708	-0.1259
Montane_PCA	0.5707	-0.0676		
Soil_cation	0.0277	0.1942	-0.5913	0.6299
Developed_2001	-0.2972	-0.8534		
Open_water_2001	0.1567	0.0601	-0.0886	-0.2593
Temp_range			-0.6985	0.4292
Dam	0.6041	-0.0832	0.3967	0.0067
Delta_wetland				
Agriculture_2001	-0.0806	0.5346	-0.0712	0.1609
Forested_2001	0.1521	0.7167		
Delta_developed	-0.1008	-0.4023	0.2015	-0.4107
Delta_forested	0.0069	0.1382	0.0078	0.3833
Delta_agriculture			0.0079	0.2401
Delta_open_water			0.1373	-0.0646
Annual_precip				
ma2	1.7570	0.1185	1.4486	0.9119
ma3	-1.7064	-0.0915	-1.5398	0.1196
fl3	-1.3945	0.4404	-0.9952	-0.4703
fh7	-1.6330	-0.4661	-1.5140	0.2362
dl16	-0.5716	1.1989	-0.9390	0.8092
dh15	0.3757	1.3616	-0.8894	0.9681
ta2	1.6011	-0.2382	1.3728	0.7305
tl2	0.5006	-0.3925	0.2205	-0.2074
ra1_div_ma2	-1.6017	-0.4919	-1.5039	-0.1567
ra8	0.4742	-1.1547	1.0039	-0.8161
Variance Explained	40.2%	13.3%	43.9%	12.0%