Landscape variables characterize thermal ~~stability~~ in Southeastern US Brook Trout streams

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1 Abstract

Thermal stability is a critical influence on aquatic ecosystems. As climate change brings heat waves and droughts to coldwater ecosystems across the globe, habitat offering cool and stable water temperatures will be critical thermal refuge for aquatic organisms. Air temperatures, groundwater, and shading can all impact stream thermal stability, but little is known about the influence of local landscape. We use the maximum slope of the logistic function relating paired weekly mean air temperature and stream temperature as an index of stream thermal stability. We use public, national data to predict this thermal stability at 203 sites in the southeastern USA using a Bayesian hierarchical framework. Stream thermal stability was best explained by landscape and hydrologic variables including groundwater, winter water velocity, land cover, and soil moisture. Together, these factors explained 98% of variation in thermal stability and allowed the determination of habitats with highly stable and cool water temperatures. We further expand on our findings to predict thermal stability at unsampled sites throughout the study area. By identifying thermal refugia, our analysis will help managers conserve priority habitats and the populations that inhabit them.

2 Introduction

Water temperature is a critical component of freshwater ecosystems, determining species ~~assemblages~~, organismal growth, ~~and overall~~ ecosystem ~~health~~ (Caissie, 2006). ~~It affects both primary and secondary productivity (Poff et al., 2002). Most~~ aquatic organisms have ranges of thermal tolerance (Coutant, 1977; Ebersole et al., 2001). As global climate change brings increased air temperatures, water temperatures will similarly rise (Pörtner et al., 2022; van Vliet et al., 2013). High water temperatures will be exacerbated by the summer droughts expected in many temperate ecosystems. In conjunction with land use changes, invasive species, and altered hydrologic regimes, climate change will have significant adverse effects on aquatic ecosystems (Poff et al., 2002; Wagener et al., 2010).

In the southeastern USA, brook trout (*Salvelinus fontinalis*) are a valu~~able~~ native salmonid facing range-wide declines (Flebbe et al., 2006; Hudy et al., 2008). They are highly sensitive to changes in water temperature, and cannot withstand temperatures higher than 22-24°C (Eaton et al., 1995; Wehrly et al., 2007). Thermal refugia allow them to persist when ambient stream temperatures exceed those at which they ~~can grow, respirate, or survive~~ (Hitt et al., 2017; Petty et al., 2012; Trego et al., 2019). This habitat preference means that brook trout thrive where they find cool, buffered water temperatures. The ability to identify and predict thermally suitable brook trout habitat is of the utmost importance for managers. Brook trout habitat in the southeastern USA is expected to experience acute effects of climate change (Ingram et al., 2013). As climate change brings warmer and more variable water temperatures to this region, brook trout and other sensitive aquatic taxa will increasingly reach or approach the limits of their thermal tolerances (Ingram et al., 2013).

Stream temperature~~, and the variability thereof,~~ is known to be influenced by a multitude of atmospheric, hydraulic, and landscape characteristics and processes (Caissie, 2006; Poole & Berman, 2001; Webb et al., 2008). Solar radiation and atmospheric air temperatures transfer heat into streams, while surfacewater, groundwater, and anthropogenic wastewater also interact with stream temperatures (Kelleher et al., 2012; Lalot et al., 2015). These influences may be modified by local hydrology, riparian shading, and even local landcover (Chang & Psaris, 2013; Dugdale et al., 2018; Garner et al., 2015; Mayer, 2012). Local air temperature commonly used to generalize atmospheric thermal influences on water temperature (Caissie et al., 1998; Mohseni et al., 1998a; Stefan & Preud'homme, 1993).

Thermal sensitivity, the relationship between water temperature and local air temperature, is an established measure of the thermal variance of a stream (Beaufort et al., 2020; Kelleher et al., 2012). It is also an important indicator of how water temperatures will respond to a warming climate. The concept encapsulates the resulting change in water temperature that results from a given change in air temperature. This relationship can represented by linear or nonlinear (i.e. logistic) regression, the fit of which depends on the streams in question, as well as the range of temperatures measured (Erickson & Stefan, 2000; Mohseni et al., 1998b; Mohseni & Stefan, 1999). In locations where air temperatures frequently dip below freezing, linear models can underpredict water temperatures. Also important for quantifying thermal sensitivity is the time scale at which air and water temperatures are summarized: depending on local hydrology, water temperatures can lag behind air temperatures by anywhere from hours to weeks (Stefan & Preud'homme, 1993). Most studies concur that increasing the temporal scale of summary results in higher correlation between air and water temperatures (Caissie et al., 2001; Webb & Nobilis, 1997), with the best fits typically corresponding to weekly time scales (Kelleher et al., 2012).

While work relating stream temperatures to air temperatures has been ongoing since at least the 1980s (Crisp & Howson, 1982; Erickson & Stefan, 2000; Mackey & Berrie, 1991; Mohseni et al., 1998a, 1999; Morrill et al., 2005; Stefan & Preud'homme, 1993; Webb et al., 2008; Zhu et al., 2018), less common are works relating thermal sensitivity to the mediating effects of local landscape and hydrology (Chang & Psaris, 2013; Tague et al., 2007; Toffolon & Piccolroaz, 2015). Previous research typically tests the influence of a small number of factors and has identified groundwater inflows, riparian shading, stream size, and ~~even~~ local geology as potential mediators of thermal sensitivity (Beaufort et al., 2020; Kelleher et al., 2012; Tague et al., 2007)~~, however these influences vary greatly by study area~~. Studies that investigate drivers of thermal sensitivity at regional scales and offer scaleable and transferable methods are rare (Beaufort et al., 2020; Mayer, 2012). Furthermore, researchers are often limited by stream temperature measurements that only exist in lower reaches of stream networks where monitoring gauges are located. This often requires pairing stream temperature observations with modeled air temperature measurements or those taken from afar. No study has yet been performed that employs spatially co-located and paired temperature measurements in headwater stream networks.

Here, we use a novel method to characterize landscape and hydrologic influence on stream thermal sensitivity across the native range of brook trout in the south~~eastern~~ USA. We opt for a segment-scale approach to identify and predict thermally buffered stream segments using an extensive dataset of paired air and water temperature measurements. Our study aims were threefold. First, we compared the fit of linear versus logistic regressions of weekly temperature summaries in representing the relationship between stream temperature and local air temperature. Because of its ability to represent the nonlinear behaviors of water at high and low air temperatures, we hypothesized that logistic regression would better represent the relationship. Second, we used widely available landscape and hydrologic metrics to identify drivers of stream thermal sensitivity. We predicted that measures of groundwater would be the strongest predictors of thermal sensitivity. Lastly, we predicted thermal sensitivity at unsampled brook trout habitat across the southeastern USA, using these predictions to identify both vulnerable and resilient brook trout habitat. In addressing these aims, we employed a multiyear dataset of over 200 paired stream and air temperature measurements spanning the range of brook trout in the southeastern USA.

Table 1: Summary statistics for site characteristics and temperatures (2011 - 2015). Sources: USDA Forest Service, USGS NHDPlus.

	Mean	SD
Channel ~~S~~lope (%)	3.8	4.1
Catchment area (km^2)	5.2	8.1
Elevation (m)	655.8	250.2
Stream order	2.0	1.0
Weekly ~~M~~ean ~~Air T~~emperature (C)	11.0	7.9
Weekly ~~M~~ean ~~W~~ater ~~T~~emperature (C)	11.4	5.8

3 Methods

3.1 Dataset and Study Area

We ~~considered~~ paired air and water temperature data from 203 sites ~~throughout~~ the southern Appalachian region of the USA (Fig. 1). Sites were located in randomly selected subwatersheds identified as capable of supporting populations of brook trout [~~*Salvelinus fontinalis*~~; Eastern Brook Trout Joint Venture (2006)]. ~~Located at the downstream outlet of the subwatersheds,~~ at each site a logger underwater was paired with a logger affixed to the bank or a tree. Stream and air temperatures were measured every 30 minutes using remote loggers (Onset Computer Corporation, Bourne, MA 02532). Loggers were deployed from 2011 to 2015. For ~~model fitting~~, we summarized temperatures to weekly averages.

Each site was linked using a GIS to the National Hydrography Dataset [NHDplus v2.1; U.S. Geological Survey (2016)] stream segment on which it was located. Using the NHDplus COMID code for each segment, we then accessed associated landscape metrics from the NHDplus and the Environmental Protection Agency StreamCat database (Hill et al., 2016). Together, these sources contributed 174 variables for each segment.

3.2 Principal Components Analysis

We performed a Bayesian principal components analysis (PCA) of the segment-level NHDplus and StreamCat predictors at 8,660 sites of known brook trout habitat ~~obtained through~~ the USGS' EcoSHEDS (www.usgs.gov/apps/ecosheds) ~~and from~~ the Eastern Brook Trout Joint Venture (Eastern Brook Trout Joint Venture, 2006). Landscape variables were centered and scaled. We used Bayesian principal components analysis (BPCA) due to its ability to take N/A values in inputs (Bishop, 1998; Nounou et al., 2002). Analysis was completed using the "pcaMethods" package in R (R Core Team,

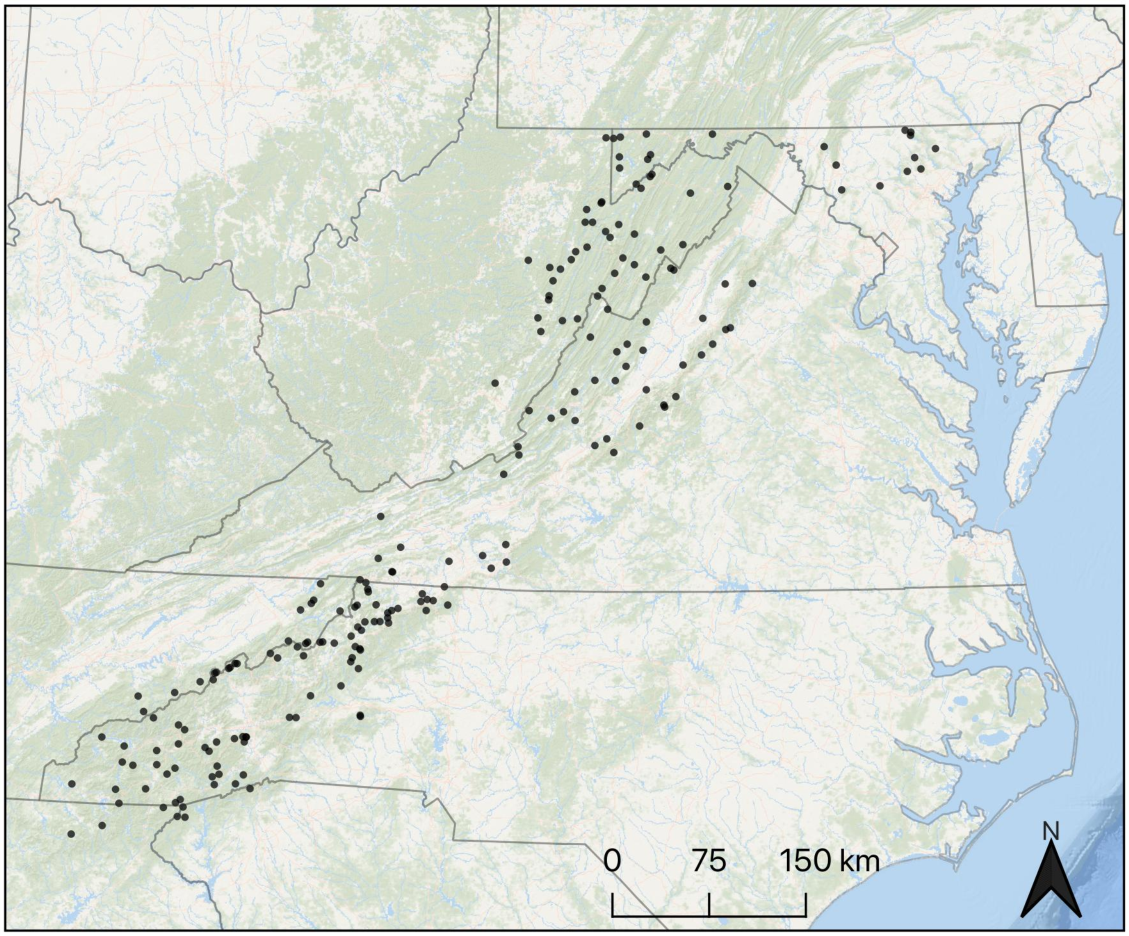

Figure 1: ~~Map~~ of 203 sites where paired air and stream temperature data were collected from 2011-2015. Stream and air temperatures were measured every 30 minutes ~~using paired remote loggers (Onset Computer Corporation, Bourne, MA 02532)~~. Sites were located at the downstream outlets of randomly selected subwatersheds identified as capable of supporting populations of brook trout (*Salvelinus fontinalis*, Eastern Brook Trout Joint Venture, 2006).

2022; Stacklies et al., 2007). We then extracted the top ten loadings by absolute value for the first five principle components (cumulative r^2: 0.61). Lastly, we extracted PCA scores for each of the 203 stream segments where ~~we had~~ temperature ~~data~~.

3.3 Hierarchical Model

We used two Bayesian hierarchical models to infer stream segment thermal sensitivity and the effects thereupon of local landscapes. We compared linear and logistic models fit to weekly maximum temperatures. By ~~fitting extracting~~ the slopes of these functions, we gain first-order estimates of the relationship between air and water temperatures (Beaufort et al., 2020; Erickson & Stefan, 2000; Kelleher et al., 2012; Morrill et al., 2005; Webb & Nobilis, 1997). ~~We cleaned data by removing observations where air temperatures were missing.~~ While nonlinear regression is often selected over linear regression for this type of modeling due to the established nonlinear behaviors of water temperature at high and low air temperatures (Mohseni et al., 1998a), we nonetheless elected to consider linear regression as it occasionally produces better fits than nonlinear regression (Beaufort et al., 2020). For the linear regression, we removed observations where air temperatures were below 0°C~~. For our linear model, we~~ fit observed water temperature T_W (° C) at stream segment $i = 1, ..., 168$ and day/week $t = 1, ..., T$

$$\mathrm{T}_{Wi,t} \sim \mathrm{normal}(g(\alpha_i, \beta_i, \mathrm{T}_{Ai,t}), \sigma^2) \tag{1}$$

where $\sigma \sim \mathrm{uniform}(0, 10)$ and $g(\alpha_i, \beta_i, \mathrm{T}_{Ai,t})$ is a linear function of observed air temperature T_A (°C) and the top five principle components of landscape variables:

$$g(\alpha_i, \beta_i, \mathrm{T}_{Ai,t}) = \alpha_i + \beta_i \mathrm{T}_{Ai,t}. \tag{2}$$

β_i, the slope of the linear air-water temperature relationship at each site, arises from $\beta_i \sim \mathrm{normal}(g(\theta_l, \mathrm{PCA}_{l,i}), \sigma^2_\beta)$ where $\sigma_\beta \sim \mathrm{uniform}(0, 10)$ and $g(\theta_l, \mathrm{PCA}_{l,i})$ for l in $1, ..., 6$ is the linear function

$$g(\theta_l, \mathrm{PCA}_{l,i}) = \theta_1 \mathrm{PCA}_{1,i} + \theta_2 \mathrm{PCA}_{2,i} + \theta_3 \mathrm{PCA}_{3,i} + \theta_4 \mathrm{PCA}_{4,i} + \theta_5 \mathrm{PCA}_{5,i} + \theta_6 \mathrm{PCA}_{6,i}. \tag{3}$$

$\boldsymbol{\theta}$, the contribution of each principal component to thermal sensitivity, arises from $\theta_l \sim \mathrm{normal}(0, 100)$.

We also implemented a nonlinear model to relate observed air and water temperatures. ~~We consider this function due to the established nonlinear behaviors of water temperature at high and low air temperatures.~~ The relationship between water temperate and air temperature decouples in freezing conditions where water begins to form ice (Morrill et al., 2005). Aberrations from the linear relationship have also been shown for high air air temperatures and those just above freezing (Mohseni & Stefan, 1999). Following Mohseni et al. (1998a), we replace Eq. (2) with

$$g(\epsilon_i, \zeta_i, \phi_i, \kappa_i, \mathrm{T}_{Ai,t}) = \epsilon_i + \frac{\zeta_i - \epsilon_i}{1 + e^{\phi_i(\kappa_i - \mathrm{T}_{Ai,t})}}, \tag{4}$$

where ϵ_i represents the minimum stream temperature (°C) at site i, ζ_i the maximum stream temperature (°C), κ_i the air temperature at the inflection point of the function (°C), and ϕ_i a measure of the slope of the function at κ_i (°C$\hat{}^{-1}$). Similar to β_i in (2), ϕ_i arises from $\phi_i \sim \mathrm{normal}(g(\theta_l, \mathrm{PCA}_{l,i}), \sigma^2_\phi)$ where $\sigma_\phi \sim \mathrm{uniform}(0, 10)$ and $g(\theta_l, \mathrm{PCA}_{l,i})$ for l in $1, ..., 6$ is (3). Following Mohseni et al. (1998a), the maximum slope of the air-water temperature relationship (β_i) at site i can be calculated from the exponent ϕ_i using the equation

$$\beta_i = \frac{4\tan\phi_i}{\zeta_i - \epsilon_i}. \tag{5}$$

We visually evaluated spatial structure in thermal sensitivity by plotting semivariograms of ~~model~~ β using the 'geoR' package in R (Ribeiro Jr et al., 2022).

We used a derived quantity, C_β, to ~~calculate the effect of landscape variables on thermal sensitivity at the 203 sites~~. C_β compares the estimated variance in thermal sensitivity of a model including principal components to predict air-water temperature slopes to the estimated variance in thermal sensitivity of a null model~~, where βs are simply estimated~~. Following Grosbois et al. (2009), we calculate C_β as

$$C_\beta = 1 - \frac{\hat{\sigma}^2_\beta(\mathrm{res})}{\hat{\sigma}^2_\beta(\mathrm{tot})}, \tag{6}$$

where $\hat{\sigma}^2_\beta(\mathrm{res})$ is the estimated variance from the full model and $\hat{\sigma}^2_\beta(\mathrm{tot})$ is the estimated variance from the null model. Assuming that the principal components explain some variation in slopes, $\hat{\sigma}^2_\beta(\mathrm{res})$ will be lesser than $\hat{\sigma}^2_\beta(\mathrm{tot})$, making C_β ~~a value~~ between 0 and 1~~. Small C_β values indicate low variance explained by the principal components, while l~~arge C_β values indicate more variance explained by the principal components.

To evaluate the performance of our models, we completed posterior predictive checks for the test statistics of mean and coefficient of variation. These checks test for lack of fit using Bayesian p-values, defined as the probability that simulated data are more extreme than the observed data (Gelman et al., 2004). Using this method, models with a ~~lack of~~ fit produce Bayesian p-values close to 0~~ or 1~~. Models were compared using the deviance information criterion (DIC), root mean square error (RMSE) of estimation, and R^2. DIC is Bayesian analogue to AIC (Spiegelhalter et al., 2002). Lower DIC and RMSE values indicate better relative and absolute model fit of those considered, while higher R^2 values indicate greater variance explained. We implemented our models utilizing Markov Chain Monte Carlo (MCMC) sampling using JAGS with the 'jagsUI' package in R (Kellner, 2021). We provide code in online supplements. After a burn-in period of 1,000 samples, three chains were run until 5,000 iterations were reached. We report posterior means as point estimates and 95% highest posterior density intervals as estimates of uncertainty.

3.4 Thermal Sensitivity Predictions and Gap Analysis

We predicted thermal sensitivity at unsampled brook trout habitat throughout the ~~southeast USA~~. In Section 3.2, we calculated principal components for ~~nearly 9,000~~ stream segments of known brook trout habitat. Using these principal components and posterior distributions for $\boldsymbol{\theta}$ from (3), we calculated ϕ_i for each segment. ~~From there, we used (5) to estimate thermal sensitivity at these unsampled sites~~. We interpolated minimum and maximum water temperatures at ~~BKT habitat sites~~ by kriging using the *spPredict* function ~~from~~ the spBayes package (Finley et al., 2015). ~~The mean structures of the~~ water temperature ~~extremes~~ were modeled using a linear combination of latitude, longitude, and elevation (m)~~;~~ and the spatial structures were modeled using an exponential covariance function based on pair-wise Euclidean distances~~ between sites~~. We specified diffused priors for all model parameters, and used posterior mean predicted temperatures for subsequent analyses.

~~Assuming that lower thermal sensitivity equates to better habitat for coldwater organisms such as brook trout,~~ we performed a gap analysis (Jennings, 2000) to evaluate the proportion of preferred thermal habitat that lies in conserved areas. Gap analyses allow the identification of valuable habitat that is unconserved. We accessed a shapefile of protected areas in the study area from the US Geological Survey's Protected Areas Database (*PAD-US 3.0*, 2022). We included protected areas with USGS Gap Analysis Project Status Codes 1-3. This includes at the least protection from conversion of natural land cover and at the most National Park or Wilderness Area designation. In a GIS (QGIS Development Team, 2023), we clipped all USGS NHDplus stream segments (U.S. Geological Survey, 2016) that were in these protected areas. We then defined preferred thermal habitat as the lowest 25th percentile of predicted thermal sensitivity values. Finally, we calculated the proportion of preferred thermal habitat sites that are located on these stream segments within protected areas.

4 Results

4.1 Principal Components Analysis

The first principal component was dominated by estimates of monthly and annual stream flow (Table 2). The second principal component was made up of metrics of spring and summer stream velocity. The third principal component included winter stream velocity and elevation, but also incorporated estimated temperature maximums within the catchment. The fourth principal component included groundwater (baseflow and water table depth), precipitation estimates, and minimum temperatures. The fifth and final principal component was dominated by measures of soil moisture, urban and deciduous landcover, and local colluviated (unconsolidated) sediment. The first five principal components explained 60.3% of the variance in predictors (Table 2).

Table 2: Top five principal components (PCs) by variance explained (R^2). The top ten contributing variables for each principal component are included. "Q" variables refer to stream flow metrics during specified periods of the year (numbers = months and MA = mean annual), and "V" variables refer to stream velocity. Further variable definitions are available from the NHDPlus User Guide and EPA StreamCat database.

	PC1	PC2	PC3	PC4	PC5
R^2	29	12.2	8.2	7.7	3.2
Variables	QC_11,	VC_07,	Lat, Long,	VC_01,	WetIndexWs,
	QE_11,	VE_07,	BFIWs,	VE_01,	PermWs,
	QC_MA,	VC_05,	BFICat,	VA_02,	PermCat,
	QC_10,	VE_05,	PrecipWs,	VA_01,	PctUrbLo2016Ws,
	QC_06,	VA_06,	PrecipCat,	TmeanCat,	PctColluvSedCat,
	QE_MA,	VC_06,	TminWs,	VC_02,	PctColluvSedWs,
	QA_11,	VA_05,	TminCat,	VE_02,	PctUrbOp2016Ws,
	QA_MA,	VA_07,	VC_02,	TmaxCat,	PctUrbMd2016Ws,
	QE_05,	VE_06,	VE_02	TmaxWs,	PctDecid2016Ws,
	QE_04	VE_11		TmeanWs	PctDecid2016Cat

4.2 Hierarchical Models

4.2.1 Model Comparison

All parameters converged at $\hat{r}$ values of 1.1 or less. Linear and nonlinear models performed ~~quite~~ similarly, and the four metrics of model fit did not consistently favor one model over the other. The nonlinear had a slightly higher mean R^2 than the linear model (0.9 vs. 0.91), but the linear model had lower RMSE and DIC (1.66 and 89510.74 vs. 1.73 and 101342.98, Table). Posterior predictive checks were nearly identical between the two models.

Table 3: Four metrics of model fit for each of the two models tested.

	Model	RMSE	R2	DIC	PPC_mean	PPC_sd
Weekly_LM_DIC.val	Linear	1.66	0.90	89510.74	0.51	0.26
Weekly_Logistic_DIC.val	Logistic	1.73	0.91	101342.98	0.52	0.26

The logistic model had a DIC of 101342.98 and an RMSE of 1.73, compared to 89510.74 and 1.66 for the linear model. Mean R^2 for the linear model was 0.9 and mean R^2 for the nonlinear model was 0.91. Posterior predictive checks were similar for linear and nonlinear models, suggesting little evidence of lack of fit between model estimates and data. Mean Bayesian p-values for mean and standard deviation for the linear model were 0.51 and 0.26. Mean Bayesian p-values for the nonlinear model were 0.52 and 0.26.

4.2.2 Thermal Sensitivity

Linear regression slopes varied from 0.22 to 1.02. These linear slopes were highly correlated with maximum slope in the nonlinear equation (0.95, Pearson's). Slopes were heterogeneous in space (Fig. 2), and several sites had particularly low and high slopes, indicating certain habitats with thermal stability or thermal elasticity. A ~~slight~~ latitudinal gradient was apparent, with lower slopes generally present at ~~lower (~~southerly~~) latitudes~~. There was also ~~considerable spatial structure in these slopes~~ (Appendix S1)~~, indicating spatial autocorrelation in thermal stability~~. β was correlated with the range of stream temperatures experienced at a site (Appendix **??**), corroborating the idea that small β equates to thermal stability.

Correlation analysis demonstrated an association between thermal sensitivity (as measured by the nonlinear regression using weekly temperatures) and local landscape. Thermal sensitivity was most closely correlated with segment slope, baseflow index (an estimate of groundwater influence), winter flow, and stream segment location and drainage area (Table 4). Using Eq. (6), we inferred the contribution of landscape variables to the estimated slope of thermal sensitivity. Principal components of landscape variables explained 98% of variance in ϕ, the measures of the steepest slope in Eq. (4).

4.2.3 Landscape Effects on Thermal Sensitivity

Principal components of landscape characteristics varied in their influence on stream thermal sensitivity. The θ value for PC3, characterized by latitude, longitude, baseflow index, precipitation, minimum air temperature, and winter stream velocity (Table 2), was significantly negative with a posterior mean

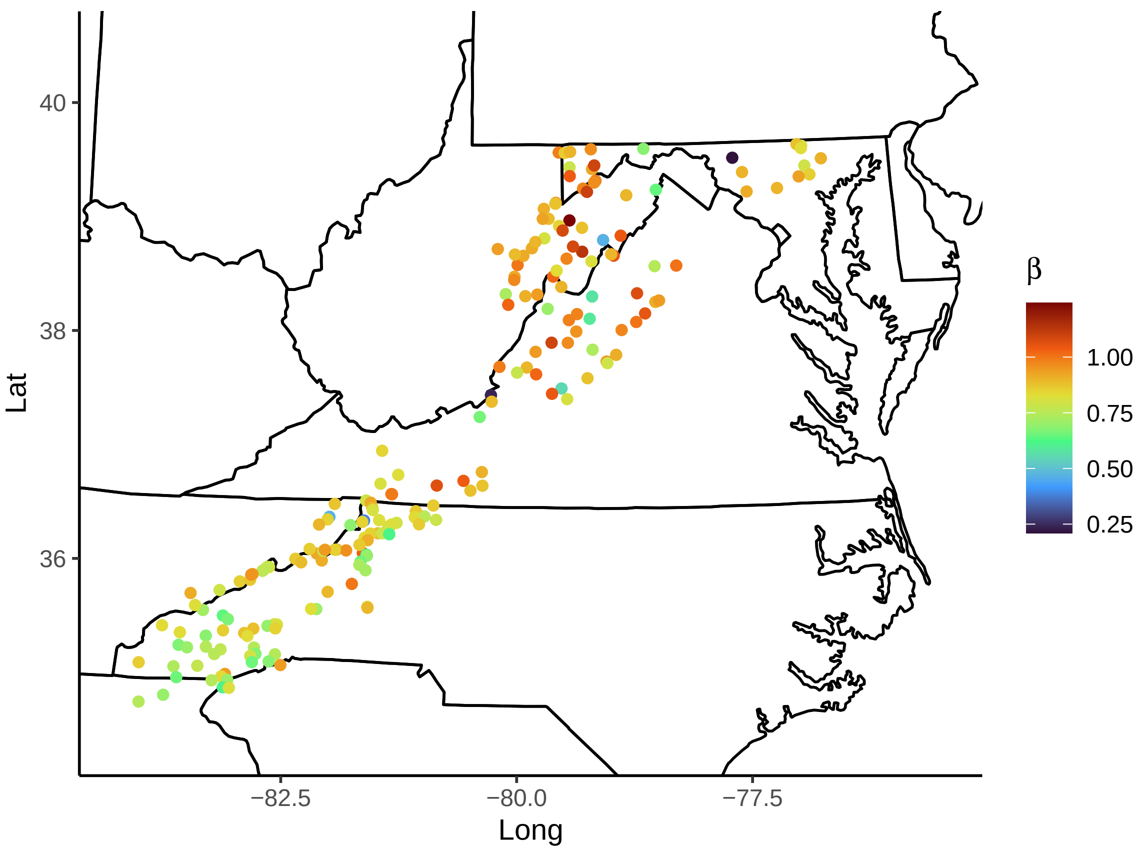

Figure 2: Air-water temperature slopes for each of 203 measurement sites. Slopes are *meta* values from the nonlear model of maximum weekly temperatures.

value of 0 (95% HPDI: 0 to 0). The θ value for PC5, characterized by soils, slope, landcover, and water table depth, was significantly positive with a posterior mean value of 0 (95% HPDI: 0 to 0). The posterior mean θ values for PC1 and PC4 were positive and for PC2 were negative, but 95% HPDI overlapped with 0 (Fig. 3).

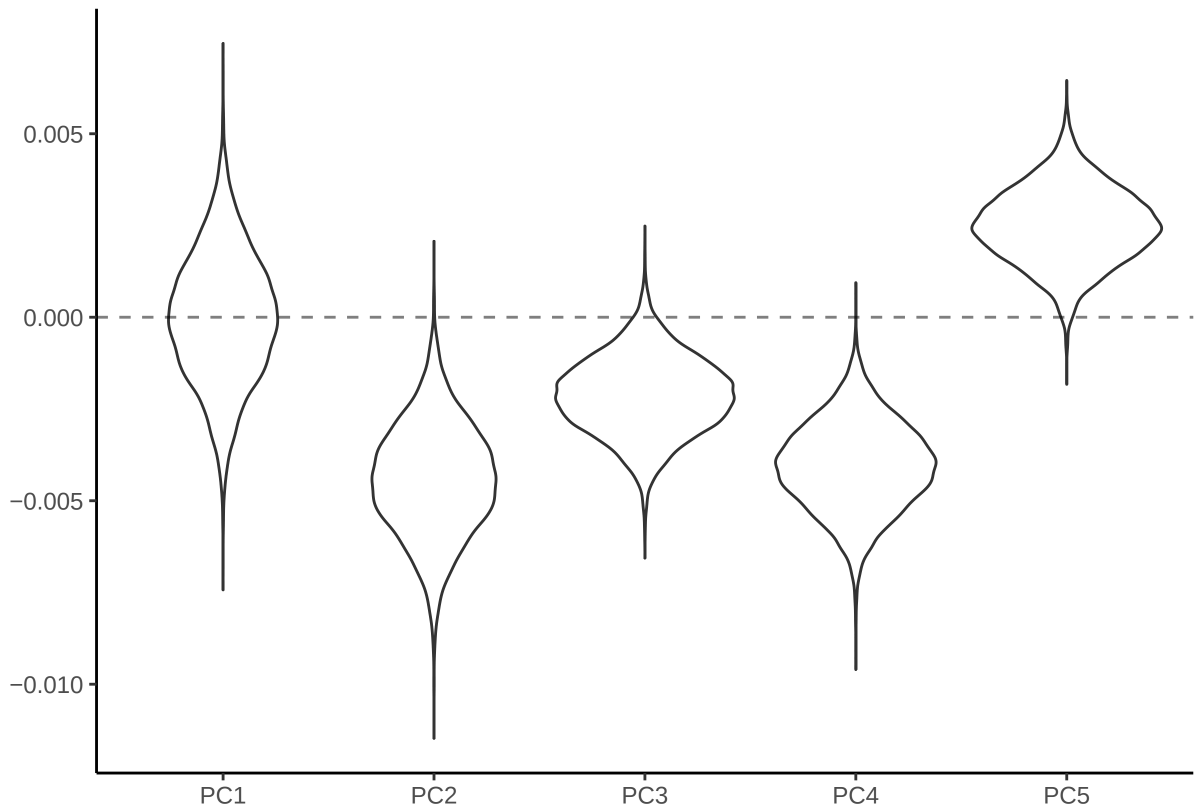

Figure 3: Full posterior distributions for ~~Eq. (3)~~ $\boldsymbol{\theta}$ values. $\boldsymbol{\theta}$ represent the contributions of principal components 1-5 to $\boldsymbol{\phi}$, the measure of maximum slope of the nonlinear equation (Eq. (4)).

4.2.4 Predictions of Thermal Sensitivity

We predicted thermal sensitivity at unsampled brook trout habitat throughout the study region using Eq. (4). Predicted $\boldsymbol{\beta}$ ranged from 0.44 (95% CI: 0.22 to 0.66) to 1.1 (95% CI: 0.95 to 1.25) at these sites, and varied greatly across the study region (Fig. 4). Among others, the Monongahela National Forest and the Great Smoky Mountains were predicted to have particularly stable stream temperatures. A latitudinal gradient in slopes was also apparent ~~here~~, further demonstrating the influence of latitude on thermal sensitivity. Our predictions highlighted several sites likely to have exceptionally stable or elastic thermal patterns. Defining preferred thermal habitat as the lowest 25th percentile of predicted thermal stability values, we found that 63% of preferred thermal habitat lies within protected areas.

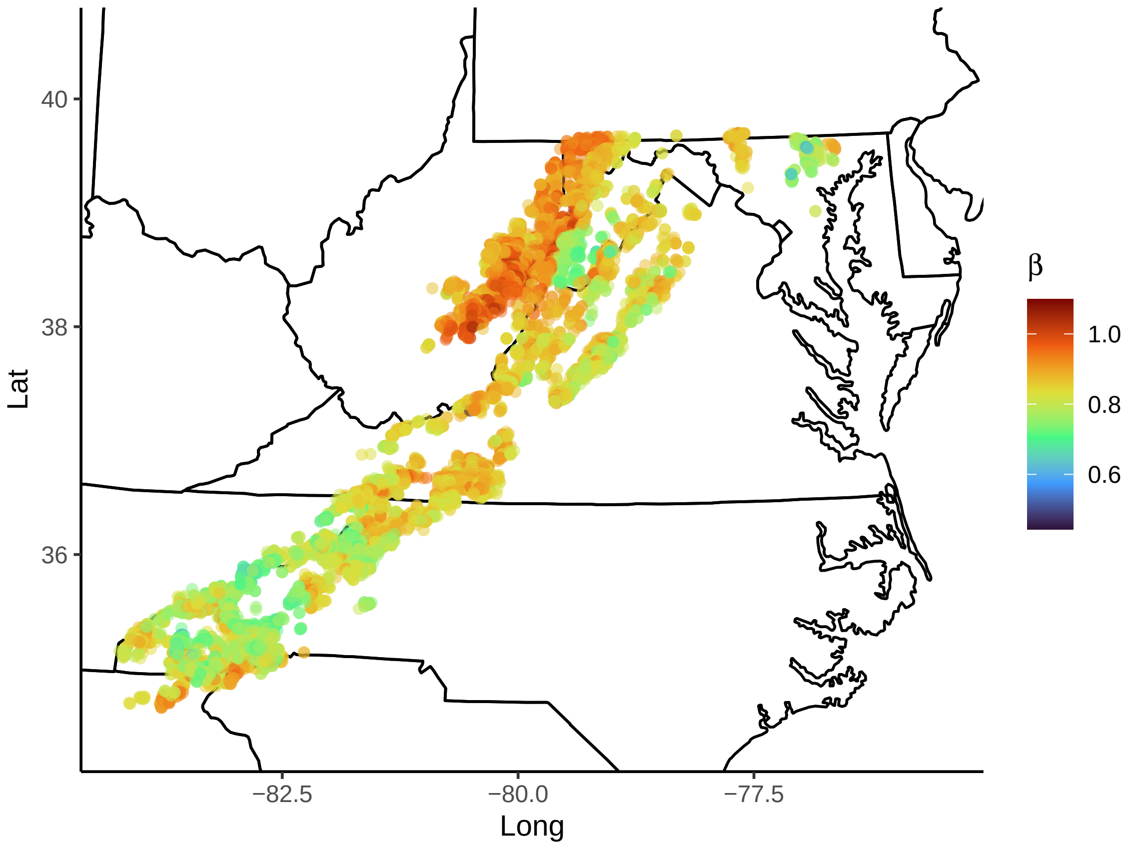

Figure 4: Predicted stream thermal stability at 8,660 sites of brook trout habitat in the southeastern USA. Thermal stability was predicted using posterior estimates from Eqs. (3) and (4), as well as spatially interpolated minimum and maximum stream temperatures.

5 Discussion

Our work represents one of the most thorough analyses to date of thermal habitat for an ~~imperiled~~ aquatic species. We used observed air and water temperatures at ~~168~~ sites throughout the south and central eastern USA to quantify stream thermal stability at multiple temporal scales using multiple models. We relate this thermal stablility to hydraulic and landscape characteristics, inferring local drivers that allow prediction at nearly 9,000 unsampled sites spanning 1,000 km of brook trout habitat. We found that a) nonlinear and linear models performed similarly in our study region; b) stream thermal stability was best explained by local hydrology such as stream velocity, baseflow, and soil moisture; and c) a slim majority of preferred thermal habitat in the southeast is currently conserved. Our results build on a solid base of investigation into stream thermal sensitivity, incorporating the influence of landscape variables and expanding analysis into new regions of interest and for species of conservation concern. We emphasize the importance of hydrological variables in determining thermal stability By using widely available data, we can make predictions of thermal habitat for a vulnerable species and work toward landscape-level conservation planning.

5.1 Landscape Influence

Landscape and hydrologic factors explained the vast majority of variance in stream thermal stability. This thermal stability, as measured by the maximum slope of logistic regression, was most highly influenced by principal component #2, incorporating summer water velocities, followed by priincipal components ___ and **, incorporating** and ___. Water velocity is related to slope, which is generally correlated with thermal stability because low slopes and velocities are more easily heated through radiation and advection. When considered in analyses of thermal sensitivity, stream velocity or slope often take a back seat to groundwater influence (Beaufort et al., 2020). However our results suggest that stream velocity may be more important in explaining stream temperature than previously thought.

We predicted that groundwater influence, as represented by baseflow index, would be the most important predictor of thermal stability (see Mayer (2012) sec. 4.2 for more details). This factor has been commonly identified elsewhere as an influence on thermal stability (Beaufort et al., 2020; Briggs et al., 2018; Johnson et al., 2020; Kelleher et al., 2012; Tague et al., 2007). In the end, the PC including baseflow index has the second strongest effect on thermal stability. This may be due to the fact that groundwater remains difficult to measure and predict over broad spatial scales such as that of our study (Kalbus et al., 2006). Also significantly influential was the principal component incorporating local sediment and landcover. Geology can be directly related to groundwater (Tague et al., 2007). Sedimentation has long been known to influence stream temperatures (Ryan, 1991), but as a landscape characteristic, sediments have not been linked to stream thermal stability. Mixed forest within the stream catchment has been identified as an important factor in creating coldwater refugia (Monk et al., 2013).

While our results support the findings of other authors - namely that groundwater can have important influence on stream thermal stability - they also lend support to hydrologic influences such as streamflow and identify novel linkages such as soil moisture. Future research should seek to identify mechanisms behind these novel influences on stream temperature.

While base flow index was highly ranked in PC ___, this PC was eclipsed by those including streamflow and landcover

5.2 Model Comparison

We found that nonlinear and linear regression performed similarly. Research is divided in its assessment of the relative fits of these two models, and differences in fit are often related to the latitude and region of the study area. Researchers at higher latitudes and cooler climates in North America generally favor the fit of logistic regression (Kelleher et al., 2012; Mayer, 2012), while work in warmer climates such as southern Europe (Beaufort et al., 2020) generally favors linear regression. Nonlinear fits such as generalized additive models (GAMs) have occasionally been favored as well (Laanaya et al., 2017). Relative fits likely vary by region because differences are mainly attributable to model behavior at high and low air temperatures where nonlinear behavior occurs. In locations where freezing air temperatures are rare (or removed for analysis), linear regressions often fit best. Where air temperatures below freezing are more common, nonlinear fits may be favored. Despite the fact that our study area was at relatively low latitudes, due to its elevation, it can experience freezing temperatures in winter. Future work should seek to establish how linear and nonlinear regressions of thermal stability compare in regions that lack freezing air temperatures.

Despite the fact that nonlinear models can sometimes better explain thermal stability, linear fits remain useful because they allow simple comparisons of slopes between studies. Our estimates of slopes for weekly linear regressions are roughly in line with those reported in previous reports (see Table 3 in Beaufort et al., 2020). Linear slopes were generally lower/higher than findings from other studies, indicating that water temperatures at trout habitat in the southeast US are more/less buffered than those in other regions.

5.3 Prediction

~~Effective management of aquatic resources depends heavily on predictive forecasting, and there is a need for informed predictions made at the broad scales at which ecological processes occur (Briggs et al., 2018). By using widely available landscape characteristics, our methods allow us to predict thermal stability at unsampled brook trout habitat throughout the southeastern USA. Given that our nonlinear model allows the inclusion of site-specific minimum and maximum water temperatures to more accurately fit the air-water temperature relationship, we chose to employ this model for predictions.~~ Predicted stream thermal stability was highly influenced by these inputs of minimum and maximum stream temperatures, as illustrated by the similarity between predicted thermal stability (Fig. 4) and predicted minimum and maximum stream temperature (Appendix S3). Our predictions identified a moderate latitudinal gradient in thermal stability, with more consistently stable water temperatures occurring in the southern half of the study region. This finding is in contradiction to the prevailing thought that northerly brook trout habitat is generally preferable in this study region, and that poor southerly habitat may mark these populations for imminent extirpation (Flebbe et al., 2006). Managers should consider that even if southerly habitat may have higher average water temperatures than northerly habitat, it may still hold value due to its thermal stability. In addition to this latitudinal gradient, we identified several areas marked by stable stream temperatures. These predicted thermal stabilities will be crucial for allocating funding and conservation resources throughout the study region. Predictions such as these can also be used to identify important thermal habitat for small-scale follow up research. Broad scale modeling of aquatic thermal habitat can be particularly useful when combined with microhabitat studies such as _____. Our work adds to a small but growing body of broad-scale thermal predictions in North America (Isaak et al., 2017; e.g., Maheu et al., 2016).

Our gap analysis revealed that a majority of thermally stable brook trout habitat in the study area already lies within protected areas. These protected areas are often highly conserved (*PAD-US 3.0*, 2022), and at the least are protected from the conversion of natural land cover to anthropogenic land cover. Conversely, this means that nearly half of this habitat remains vulnerable to human impacts and land use conversion. Brook trout are an aquatic indicator species, and they often cohabitate with other sensitive and threatened taxa (VanDusen et al., 2005; Vile & Henning, 2018). Managers and conservationists seeking to conserve land in this region should incorporate stream thermal stability into their considerations.

A common drawback of studies of thermal stablity is that air temperatures are derived from model outputs or the most convenient meteorological station (Beaufort et al., 2020; Hare et al., 2021;

Kelleher et al., 2012). This means that trends in air temperatures used for analysis may not reflect the true trends influencing stream temperature at the local scale (Kanno et al., 2014). Solar radiation and the influence of local topography have been shown to substantial influence variation in the microclimate across the landscape, particularly in mountainous areas (Aalto et al., 2017; Tscholl et al., 2022). Furthermore, weather stations are commonly situated in open, flat areas where they miss the thermal effects of topography and tree cover (De Frenne & Verheyen, 2016; Graae et al., 2012). We overcome this problem by using air temperatures measured in-situ at the same locations where water temperatures are measured. By using these paired air and water temperature loggers, our study design therefore allows the consideration of highly local atmospheric influence on stream temperature.

~~The use of PCA to reduce the number of landscape variables can limit our ability to assess the influence of any one variable on thermal stability. However, the PCA groups similar variables, meaning that distinguishing between variables contained in the same PC is not so necessary. Essentially, this is a trade-off between considering many variables to identify novel linkages and considering fewer variables to identify specific ecological relationships.~~

5.4 Final paragraph - reiterate most important finding

Thermal stability is a critical stream habitat characteristic that is influenced by local hydrologic and landscape factors. As climate change brings warmer and more variable air temperatures to temperate climates, stable and cool habitats will become important climate refugia (Jones et al., 2014). Spatially explicit predictions such as ours offer important insight into regional patterns that may not be visible from localized studies, and these can help with important conservation and management decisions. Our results support and build on previous findings relating local landscape to stream temperatures.

6 References

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7 Appendix

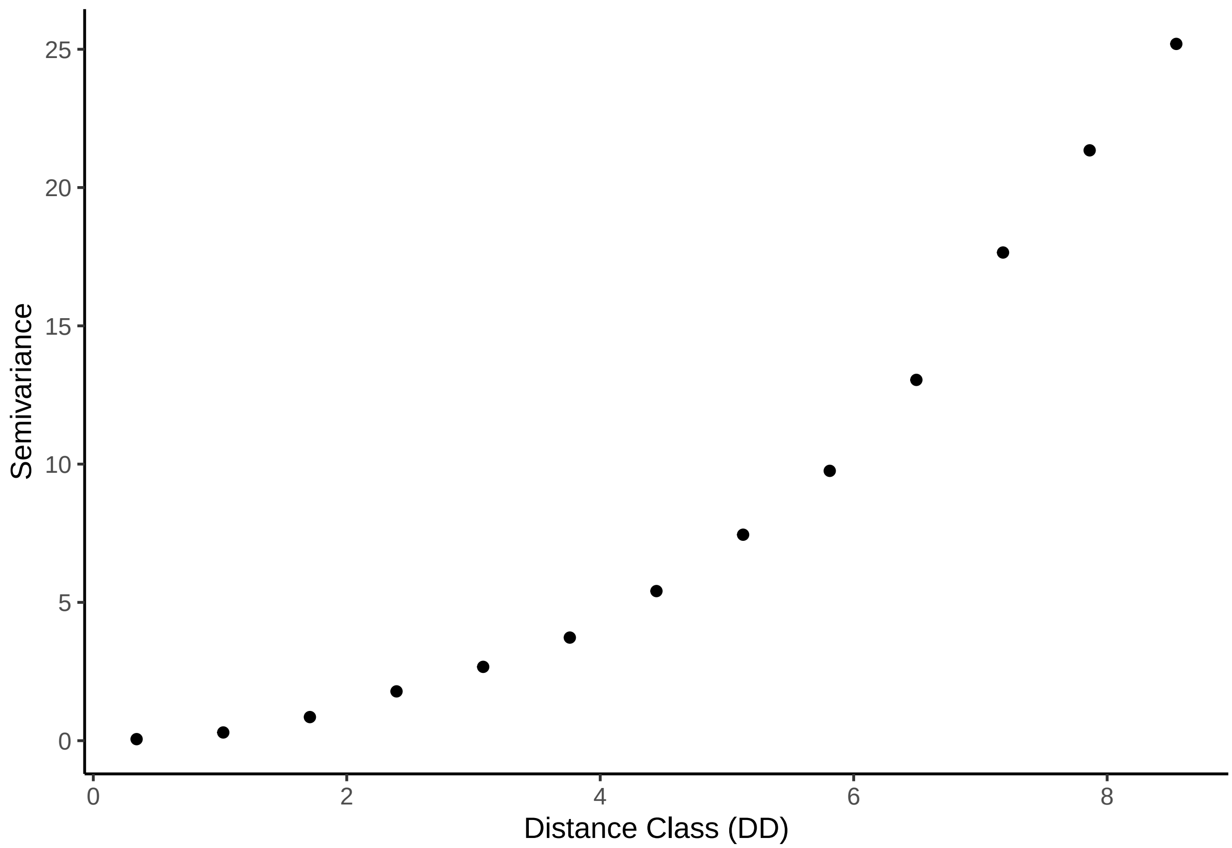

Figure S1: Semivariogram depicting spatial structure in thermal sensitivity at ~~168~~ sites. Slopes (model *etas*) are posterior means of the nonlinear model of weekly maximum temperatures.

Table 4: Top ten Spearman correlations between maximum slopes of the weekly nonlinear regression and local landscape variables. Correlations were tested for 172 segment, catchment, and watershed characteristics accessed from the USGS NHDplus and EPA StreamCat database. Abbreviations (descriptions from sources): SLOPE = Stream segment slope based on smoothed elevations, BFIWs = Baseflow index (component of streamflow attributable to groundwater) for stream segment watershed, BFICat = Baseflow index for stream segment catchment, Lat = Stream segment outlet latitude, Long = Stream segment outlet longitude, QC_02 = Estimated flow (February), QE_02 = Gauge adjusted estimated flow (February), WsAreaSqKm = Stream segment watershed area (km^2), TotDASqKM = Total upstream cumulative drainage area (km^2), = Divergence-routed cumulative drainage area (km^2). Further variable definitions are available from the NHDPlus User Guide and EPA StreamCat database.

Landscape Variable	Correlation
SurfArea	-0.5000000
RAreaHLoad	0.5000000
BFIWs	-0.4584096
BFICat	-0.4546629
Lat	0.4407088
Long	0.4099888
QC_03	0.4036784
QE_03	0.4029066
WsAreaSqKm	0.4014893
TotDASqKM	0.4014893

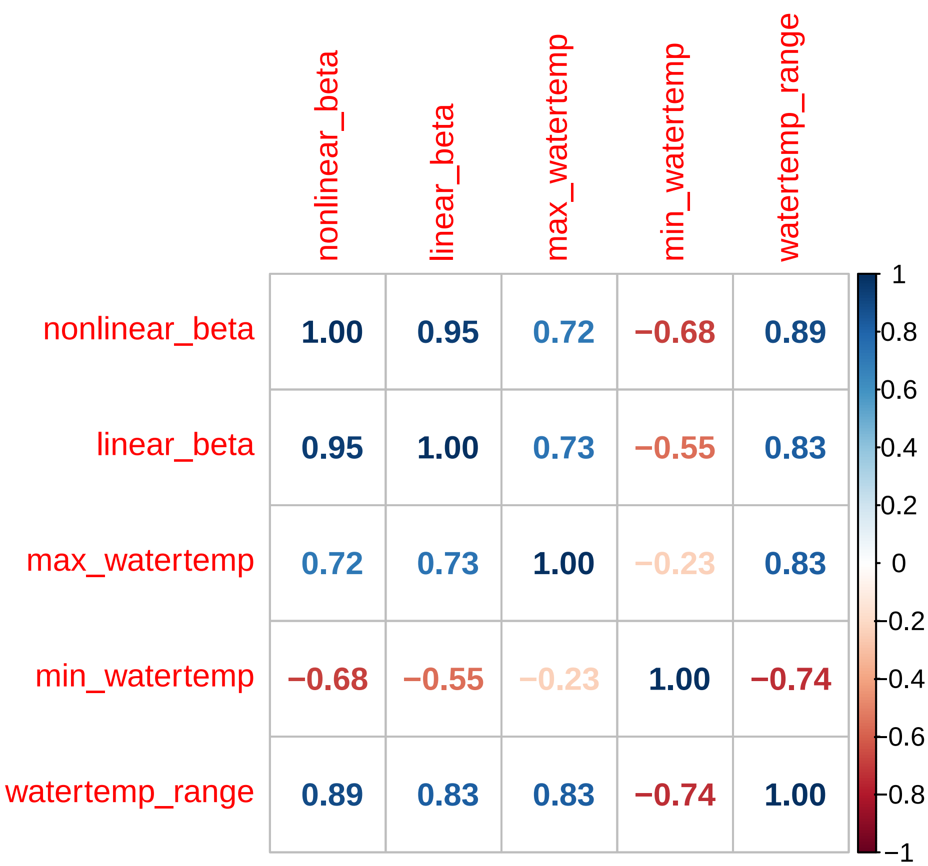

Figure S2: Pearson's correlations between nonlinear and linear model β and minimum, maximum, and range of weekly mean stream temperatures.

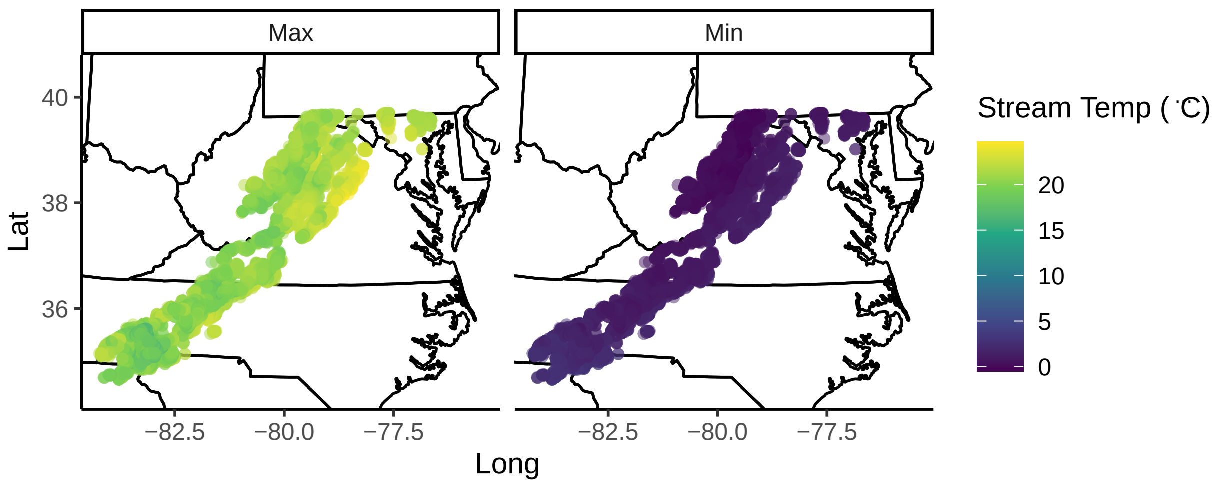

Figure S3: Minimum and maximum weekly stream temperatures at 8,660 sites of brook trout habitat. Sites were obtained through EcoSHEDS (www.usgs.gov/apps/ecosheds) and the Eastern Brook Trout Joint Venture (Eastern Brook Trout Joint Venture, 2006). Stream temperature ~~extremes~~ were spatially interpolated from measured temperatures using latitude, longitude, and elevation.