

LANDSCAPE INFLUENCES ON THERMAL SENSITIVITY AND PREDICTED SPATIAL
VARIABILITY AMONG SOUTHEASTERN USA BROOK TROUT STREAMS

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1 Abstract

7 Warming water temperature as a result of climate change poses a major threat to coldwater organisms.
8 However, the rate of warming is not spatially uniform due to surface-ground-water interactions and
9 stream and watershed characteristics. Coldwater habitats that are most resistant to warming serve
10 as ~~climate~~ refugia and identifying their locations is critical to regional aquatic conservation planning.
11 Here, we quantified the thermal sensitivity of 203 streams providing habitat for brook trout (*Salvel-*
12 *nus fontinalis*) in the southern and central Appalachian region, USA (~1,000 km), and characterized
13 their spatial variability with landscape variables available in the National Hydrography Dataset. We
14 used the maximum slope of the Bayesian logistic function relating paired weekly mean air tempera-
15 ture and stream temperature as an index of stream thermal sensitivity. Streams differed greatly in
16 thermal sensitivity and those with more resistant water temperature regimes (i.e., thermal refugia)
17 were characterized by groundwater input, southerly latitudes, low winter flows, and small watersheds.
18 Together, landscape variables derived from a principal component analysis explained 98% of variation
19 in thermal sensitivity. Using our model and spatial interpolation, we predicted thermal sensitivity at
20 8,600 stream segments potentially suitable for brook trout in the study region. ~~Climate~~ refugia were
21 more common southward presumably due to higher elevations, but they were also structured at finer
22 spatial scales. Our analysis informs prioritizing habitat conservation and restoration of this native
23 salmonid and other aquatic organisms that depend on coldwater habitats in a warming world.

2 Introduction

Water temperature is a key component of lotic ecosystems, determining species composition, organismal growth, and ecosystem functions and productivity (Caissie, 2006; Poff et al., 2002). Stream temperatures have risen in the last few decades (Kaushal et al., 2010) and will continue to rise as global climate change accelerates (Pörtner et al., 2022; van Vliet et al., 2013). Warming water temperature poses a major threat to the persistence of coldwater organisms, but warming rates are not spatially homogeneous due to surface-groundwater interactions and watershed and localized landscape characteristics (Lisi et al., 2013; Winfree, 2017). Identifying characteristics of stream habitats that offer refuge from climate warming and predicting their locations is critical to coldwater conservation planning (Ebersole et al., 2020).

However, a challenge lies in locating climate refugia for coldwater organisms over a broad geographic extent. Stream temperature is influenced by a multitude of atmospheric, hydraulic, and landscape characteristics and processes (Caissie, 2006; Lisi et al., 2015; Poole & Berman, 2001; Webb et al., 2008). Physical temperature models incorporate solar radiation, air-water heat transfer, evapotranspiration, and groundwater input [Caissie (2006); Kelleher et al. (2012); Lalot et al. (2015); sinokrot1993]. These processes may differ spatially due to local hydrology, riparian shading, and local landcover (Chang & Psaris, 2013; Dugdale et al., 2018; Garner et al., 2015; Mayer, 2012). These process-based modeling approaches are difficult to replicate at many sites, especially for predicting temperatures at unsampled sites and consequently strategizing landscape and regional conservation efforts.

Alternatively, statistical approaches based on the relationships between stream and air temperatures have proliferated to characterize thermal variation among streams (Crisp & Howson, 1982; Mackey & Berrie, 1991; Mohseni & Stefan, 1999; Stefan & Preud'homme, 1993; Zhu et al., 2018, etc.) Stream-air temperature relationships have been represented by linear (Beaufort et al., 2020; Erickson & Stefan, 2000) or nonlinear (i.e., logistic) regression (Mohseni et al., 1998; Mohseni & Stefan, 1999). The nonlinear approach is best suited to regions characterized with low ($<0^{\circ}\text{C}$) and high ($>25^{\circ}\text{C}$) air temperatures. Specifically, stream temperature typically remains above 0°C when surface ice forms in winter, and at elevated air temperature in summer, evaporative cooling mitigates warming rates (Mohseni et al., 1998; Mohseni & Stefan, 1999). Stream-air temperature relationships have been modeled ~~at everything~~ from hourly to annual time scales (Caissie et al., 2001; Sinokrot & Stefan, 1993; Stefan & Preud'homme, 1993; Webb & Nobilis, 1997), with the time lag between stream and air temperature diminishing over longer temporal scales and thus the tightest stream-air temperature

relationships at weekly scales (Kelleher et al., 2012). Sensitivity of stream temperature relative to changes in air temperature is typically used as an indicator of groundwater input, where more temporally stable stream temperature amid air temperature fluctuations signifies thermal refugia (Beaufort et al., 2020; Hare et al., 2023; Kelleher et al., 2012).

Despite our increasing knowledge of spatial variability in thermal sensitivity, few studies have undertaken to explain or predict spatial variability using readily available watershed hydrological data at the national and regional scale (Mayer, 2012; Trumbo et al., 2014) (e.g., EPA StreamCat or National Hydrography Dataset (NHD) in the USA). These broad-scale data sets inherently provide coarse-scale habitat characterization; for example, the NHD contains hydrologic data at the stream segment scale, defined as the length of streams between two confluences or from the headwater to the first confluence downstream. Thus, spatial heterogeneity within stream segments and highly localized processes (i.e., groundwater seepage) could be missed, limiting our ability to locate thermal refugia. Despite potential limitations, spatial variability in thermal sensitivity has been attributed to coarse-scale metrics such as riparian conditions, stream size, and geology (Beaufort et al., 2020; Chang & Psaris, 2013; Mayer, 2012; Tague et al., 2007; Toffolon & Piccolroaz, 2015). As broad-scale stream data become increasingly available, it is important to test their ability to explain and predict thermal sensitivity over a broad geographic extent to inform management of coldwater species of conservation concern.

Brook trout (*Salvelinus fontinalis*) are a coldwater salmonid whose native distribution covers much of eastern North America. Brook trout populations have declined greatly, particularly in their southern native range, due to anthropogenic factors such as habitat loss and fragmentation, non-native species, and introgression with hatchery fish (Hudy et al., 2008; Kazyak et al., 2022). As a coldwater species, they cannot withstand prolonged periods of water temperatures higher than 22-24 °C (Eaton et al., 1995; Hartman & Cox, 2008; Wehrly et al., 2007). Riverscapes in which brook trout can access areas with cool stream temperatures allow them to persist through heat waves and droughts (Hitt et al., 2017; Petty et al., 2012; Trego et al., 2019). Thus, the ability to identify and predict thermally suitable brook trout habitat over a long period (i.e., thermal refugia) is of great importance for prioritizing streams for conservation and restoration action such as habitat improvement, physical barrier removal, non-native trout removal, and brook trout translocations (Kanno et al., 2016; White et al., 2023). Stream temperatures have been modeled for brook trout streams in their native range, including the use of paired stream-air temperature measurements (Kanno et al., 2014; Letcher et al., 2016; Trumbo et al., 2014). However, these studies were limited in their geographical extent and we are not aware of previous work which combined paired stream-air temperature measurements with readily available

watershed and hydrological data to describe and predict thermal sensitivity of streams at the regional scale.

Here, we characterized landscape influences on stream thermal sensitivity across the native range of brook trout in the southern and central Appalachian Mountains regions, USA (~ 1,000 km), using a multi-year data set of paired stream and air temperature measurements. Located at their southernmost native range, ~~the study area is one where~~ brook trout have suffered their greatest declines (Hudy et al., 2008). Our study objectives were two-fold. First, we used widely available landscape and hydrologic metrics to identify determinants of stream thermal sensitivity with a Bayesian hierarchical model of nonlinear relationships between weekly average stream and air temperatures. Second, we used this model to predict thermal sensitivity at unsampled brook trout habitats throughout the study area. In addressing these objectives, we aimed to quantify how much thermal sensitivity varied among streams in the study area and its correlation with landscape characteristics and identify locations of thermal refugia for brook trout in a warming world.

3 Methods

3.1 Dataset and Study Area

We collected paired air and water temperature data from 203 sites in the southern and central Appalachian region of the USA (Fig. 1, Table 1). Sites in the southern Appalachians were generally situated at higher elevation than sites in the central Appalachians (mean 734 m vs. 563 m). Sites were located in randomly selected watersheds identified as capable of supporting populations of brook trout (Eastern Brook Trout Joint Venture, 2006; Li et al., 2016). **Located at the downstream outlet of the watersheds,** 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 data analysis, we summarized temperatures to weekly averages.

A common drawback of studies of thermal sensitivity 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.

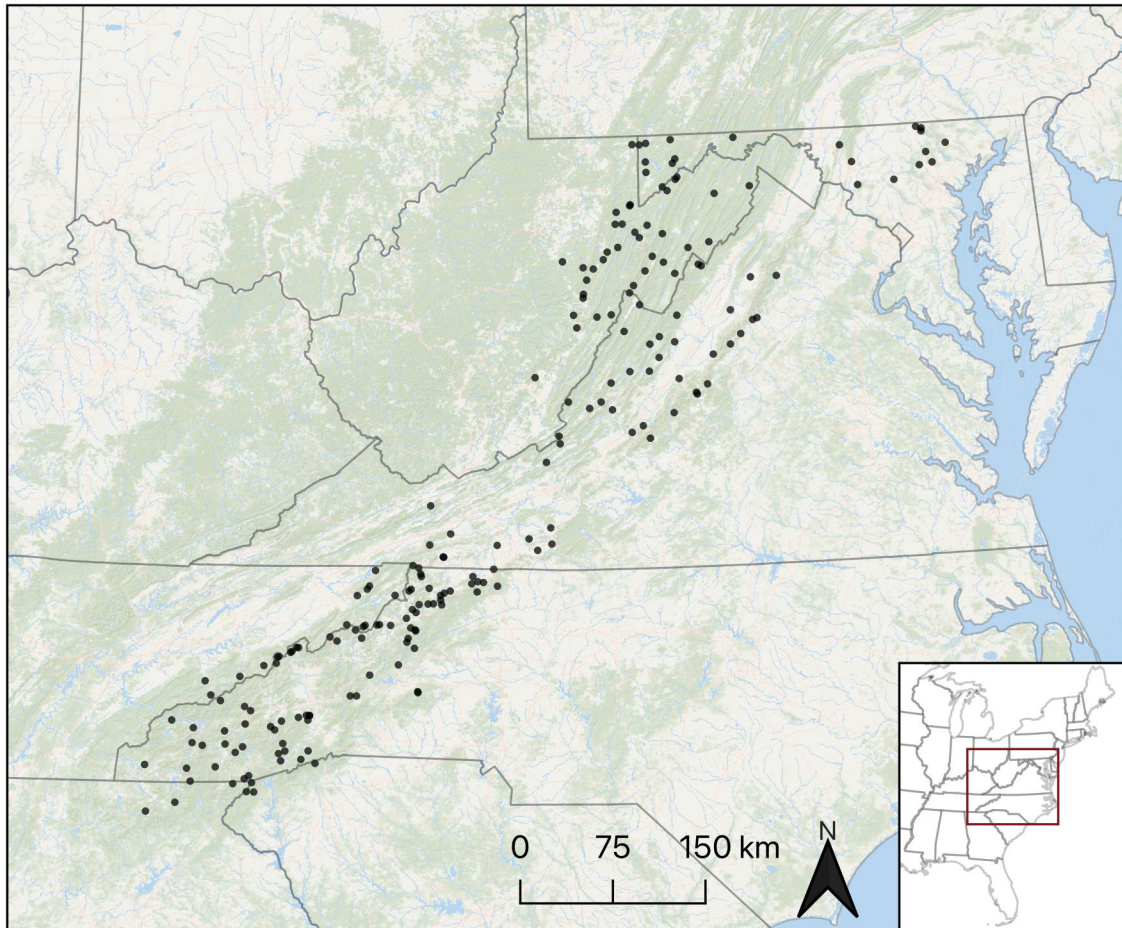


Figure 1: Map of 203 sites where paired air and stream temperature data were collected from 2011-2015. Green shading represents forested areas.

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 describing hydrology, land cover, geology, soils, and topography for each segment. While certain variables such as groundwater and stream size have well-defined influences on stream temperature (Beaufort et al., 2020; Chang & Psaris, 2013; Mayer, 2012), we chose to include all variables in order to improve predictive capacity.

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

	Mean	SD
Channel slope (%)	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 mean air temperature (C)	11.0	7.9
Weekly mean water temperature (C)	11.4	5.8

3.2 Principal Components Analysis

We performed a Bayesian principal components analysis (PCA) of the segment-level NHDplus and StreamCat predictors at 8,695 sites of known brook trout habitat identified in the USGS' EcoSHEDS (www.usgs.gov/apps/ecosheds) and by the Eastern Brook Trout Joint Venture (Eastern Brook Trout Joint Venture, 2006). We excluded sites with stream orders greater than five. 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, 2022; Stacklies et al., 2007). We then extracted the top ten loadings by absolute value for the first five principle components (cumulative r^2 : 0.60). Lastly, we extracted PCA scores for each of the 203 stream segments where temperature was measured.

3.3 Hierarchical Model

We used a Bayesian hierarchical logistic model to infer stream thermal sensitivity and the effects thereupon of local hydrology and landscapes. ~~By extracting the slope at the inflection point of the of the function; a first-order estimate of the relationship between air and water temperatures can be gained~~ (Kelleher et al., 2012; Mohseni et al., 1998; Morrill et al., 2005). We removed observations where air temperatures were missing. Adapting Mohseni et al. (1998), we fit weekly mean water temperature T_W (°C) at site $i = 1, \dots, 203$ and week $t = 1, \dots, T$ as a function of weekly mean air temperature T_A (°C) with

$$T_{W,i,t} \sim \text{normal}(\epsilon_i + \frac{\zeta_i - \epsilon_i}{1 + e^{\phi_i(\kappa_i - T_{A,i,t})}}, \sigma^2), \quad (1)$$

where ζ_i ~~is derived from~~ the maximum weekly mean stream temperature (°C) at site i , ϵ_i ~~is derived from~~ the minimum weekly mean stream temperature (°C) at site i , κ_i ~~the air-estimated~~ temperature

at the inflection point of the function ($^{\circ}\text{C}$), and ϕ_i a measure of the slope of the function at κ_i ($^{\circ}\text{C}^{-1}$).
 ϕ_i is derived from the linear function

$$\phi_i \sim \text{normal}(\theta_1 + \theta_2 \text{PCA}_{1,i} + \theta_3 \text{PCA}_{2,i} + \theta_4 \text{PCA}_{3,i} + \theta_5 \text{PCA}_{4,i} + \theta_6 \text{PCA}_{5,i}, \sigma_{\phi}^2). \quad (2)$$

where θ represents the contribution of each principal component to thermal sensitivity. The slope of the function at the inflection point (thermal sensitivity; β_i) at site i is related to ϕ_i using the equation

$$\beta_i = \frac{\phi_i * (\zeta_i - \epsilon_i)}{4}. \quad (3)$$

We visually evaluated spatial structure in thermal sensitivity by plotting semivariograms of β values using the ‘geoR’ package in R (Ribeiro Jr et al., 2022). We also estimated thermal sensitivity using linear regression, details and results for which can be found in Appendix 7.2. We used a derived quantity, C_{ϕ} , to quantify the proportion of variance in thermal sensitivity among the 203 sites explained by landscape variables. Following Grosbois et al. (2009), C_{ϕ} compares the estimated variance in thermal sensitivity of the model including landscape covariates ($\hat{\sigma}_{\phi}^2(\text{res})$) to the estimated variance in thermal sensitivity of a null model without any landscape variables $\hat{\sigma}_{\phi}^2(\text{tot})$:

$$C_{\phi} = 1 - \frac{\hat{\sigma}_{\phi}^2(\text{res})}{\hat{\sigma}_{\phi}^2(\text{tot})}. \quad (4)$$

Assuming that the principal components explain some variation in slopes, $\hat{\sigma}_{\phi}^2(\text{res})$ will be smaller than $\hat{\sigma}_{\phi}^2(\text{tot})$, making values of C_{ϕ} range between 0 and 1, with larger C_{ϕ} values indicative of more variance explained by the principal components of landscape variables.

To evaluate the performance of the model, 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 good of fit produce Bayesian p -values close to 0.5 (range 0-1). We also evaluated the model using the root mean square error (RMSE) of estimation and R^2 . Lower RMSE values indicate better model fit, while higher R^2 values indicate greater variance explained. We implemented the model utilizing Markov Chain Monte Carlo (MCMC) sampling using JAGS with the ‘jagsUI’ package in R (Kellner, 2021). We provide code in online supplements and report noninformative priors in Appendix 7.1. After a burn-in period of 1,000 samples, three chains

were run until 5,000 iterations were reached. We considered convergence as an \hat{r} value of 1.1 or less. We report posterior means as point estimates and 95% highest posterior density intervals (HPDIs) as estimates of uncertainty.

3.4 Thermal Sensitivity Predictions and Gap Analysis

We predicted thermal sensitivity at unsampled brook trout habitat throughout the study region. In Section 3.2, we calculated principal components for 8,695 stream segments of known brook trout habitat. Using these principal components and posterior distributions for θ from (6), we calculated ϕ_i for each segment. We interpolated minimum and maximum water temperatures at stream segments by kriging using the *spPredict* function in the *spBayes* package (Finley et al., 2015). The minimum and maximum water temperatures 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. We specified diffused priors for all model parameters, and used posterior mean predicted temperatures for subsequent analyses.

Finally, 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 (Gap Analysis Project (GAP), 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 resistant thermal habitat as the lowest 25th percentile of predicted thermal sensitivity values. Finally, we calculated the proportion of resistant thermal habitat sites that were 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, QE_11, QC_MA, QC_10, QC_06, QE_MA, QA_11, QA_MA, QE_05, QE_04	VC_07, VE_07, VC_05, VE_05, VA_06, VC_06, VA_05, VA_07, VE_06, VE_11	Pct, Long, BFIWs, BFICat, PrecipWs, PrecipCat, TminWs, TminCat, VC_02, VE_02	VC_01, VE_01, VA_02, VA_01, TmeanCat, VC_02, VE_02, TmaxCat, TmaxWs, TmeanWs	WetIndexWs, PermWs, PermCat, PctUr- bLo2016Ws, PctColluvSed- Cat, PctCollu- vSedWs, PctUr- bOp2016Ws, Pc- tUrbMd2016Ws, PctDe- cid2016Ws, PctDe- cid2016Cat

4.0.2 Logistic Model

~~All model parameters converged.~~ Posterior predictive checks suggested little evidence of lack of fit between model estimates and data. Mean Bayesian p-values for mean and standard deviation were 0.52 and 0.26. Nonlinear and linear (see Appendix ??) models performed quite similarly, and the three 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 (1.66 vs. 1.73, Appendix ??). Posterior predictive checks were nearly identical between the two models.

4.0.3 Thermal Sensitivity

Logistic regression slopes varied from 0.21 (95% HPDI: to) to 1.24 (95% HPDI: to), with an average slope of 0.85 (Fig. 2). These values were correlated with the range of stream temperatures experienced at a site (Appendix S2), demonstrating the utility of this metric as a measure of thermal sensitivity. Logistic regression slopes were also highly correlated with slopes from the linear regression (0.95, Pearson's). Slopes were heterogeneous in space (Fig. 3), and several sites had particularly low and high slopes, indicating habitats with thermal stability or thermal elasticity. When plotted on a map, a latitudinal gradient was apparent, with lower slopes generally present at southerly sites. There was also evidence of spatial autocorrelation in thermal sensitivity (Appendix S1), where nearer sites had more similar thermal sensitivity than farther sites. This resulted in clustering of β values in Fig. 3).

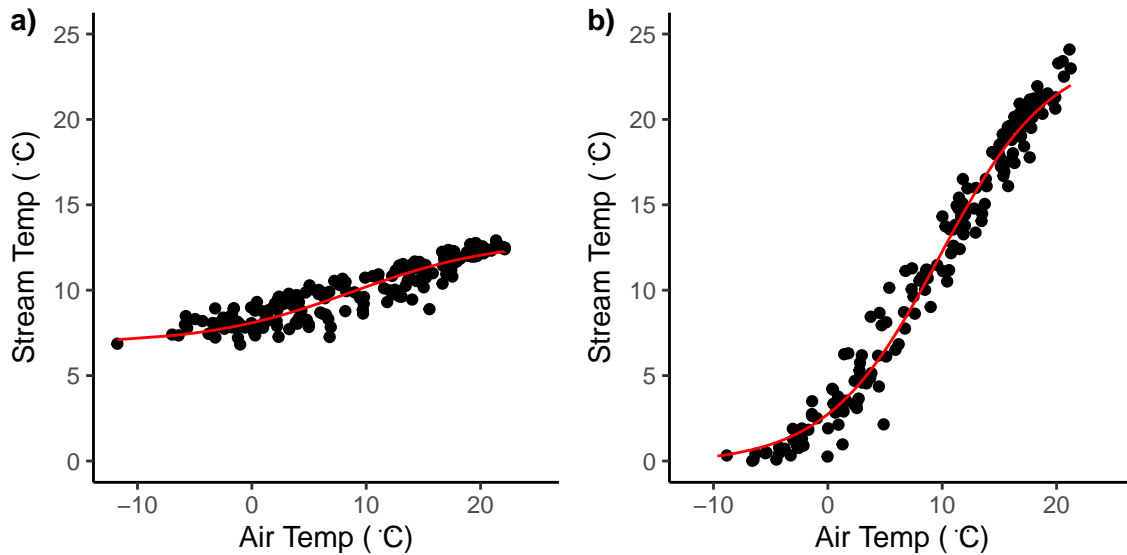


Figure 2: Logistic regression fits for a) Ewin Run near Laurel Branch, WV, USA and b) the Blackwater River near Cortland, WV, USA. Black dots represent paired weekly average temperatures and red lines represent logistic regressions.

A correlation analysis (Spearman) revealed that stream thermal sensitivity was positively correlated with baseflow index (0.45) and negatively correlated with latitude (-0.44), March streamflow (-0.4), and watershed area (-0.4). Using Eq. (4), we inferred the contribution of landscape variables to the estimated slope of thermal sensitivity. Principal components of landscape variables explained 88% of variance in ϕ , the measures of the steepest slope in Eq. (1).

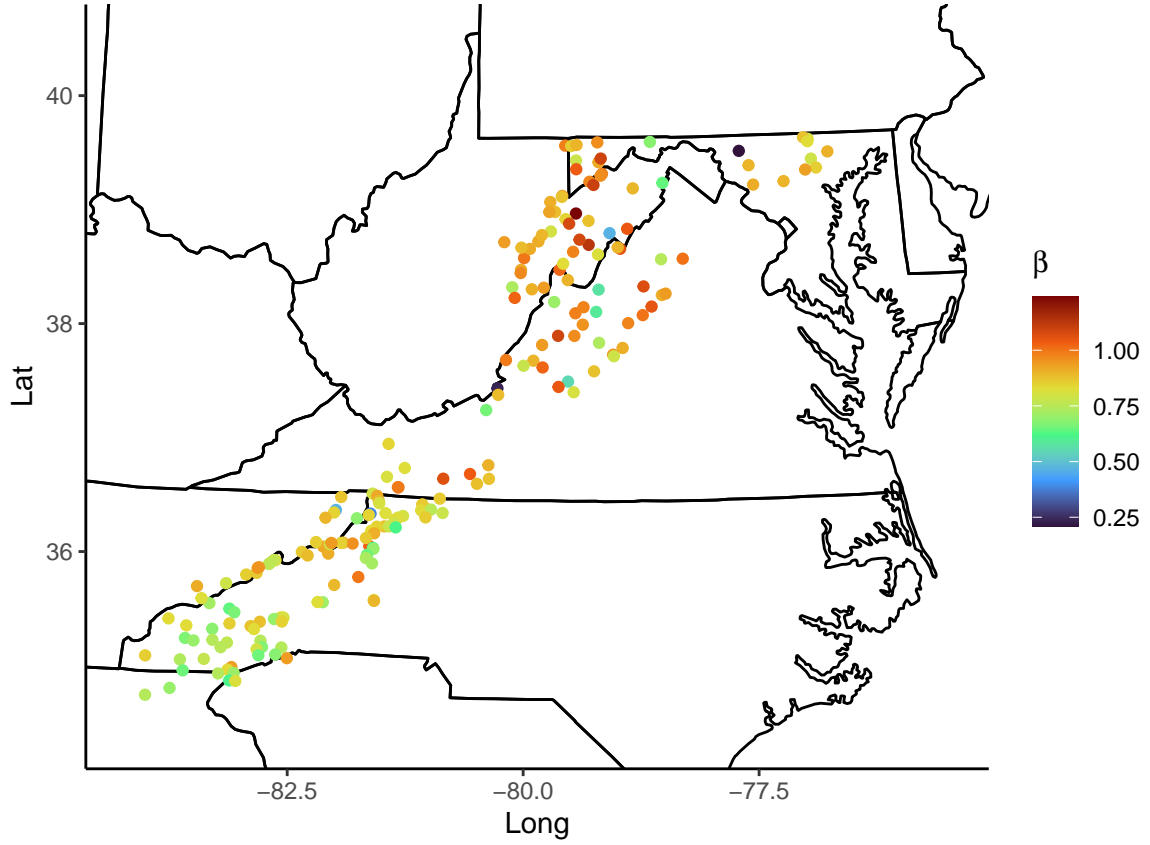


Figure 3: Air-water temperature slopes for each of 203 measurement sites. Slopes are β values from the nonlinear model of weekly mean water temperatures, with smaller beta values equating to less sensitivity to changes in air temperatures (i.e., thermal refugia).

4.0.4 Landscape Effects on Thermal Sensitivity

Principal components of landscape characteristics varied in their influence on stream thermal sensitivity. θ values for PC2, PC3, and PC4 (Table 2) were small, but significantly negative with posterior means of -0.004 (95% HPDI: -0.007 to -0.0015; Fig. 4), -0.002 (95% HPDI: -0.004 to -0.0001), -0.004 (95% HPDI: -0.006 to -0.002). The posterior distribution of θ for PC5 was similarly small but significantly positive, with a mean of 0.002 (95% HPDI: 0.0004 to 0.004).

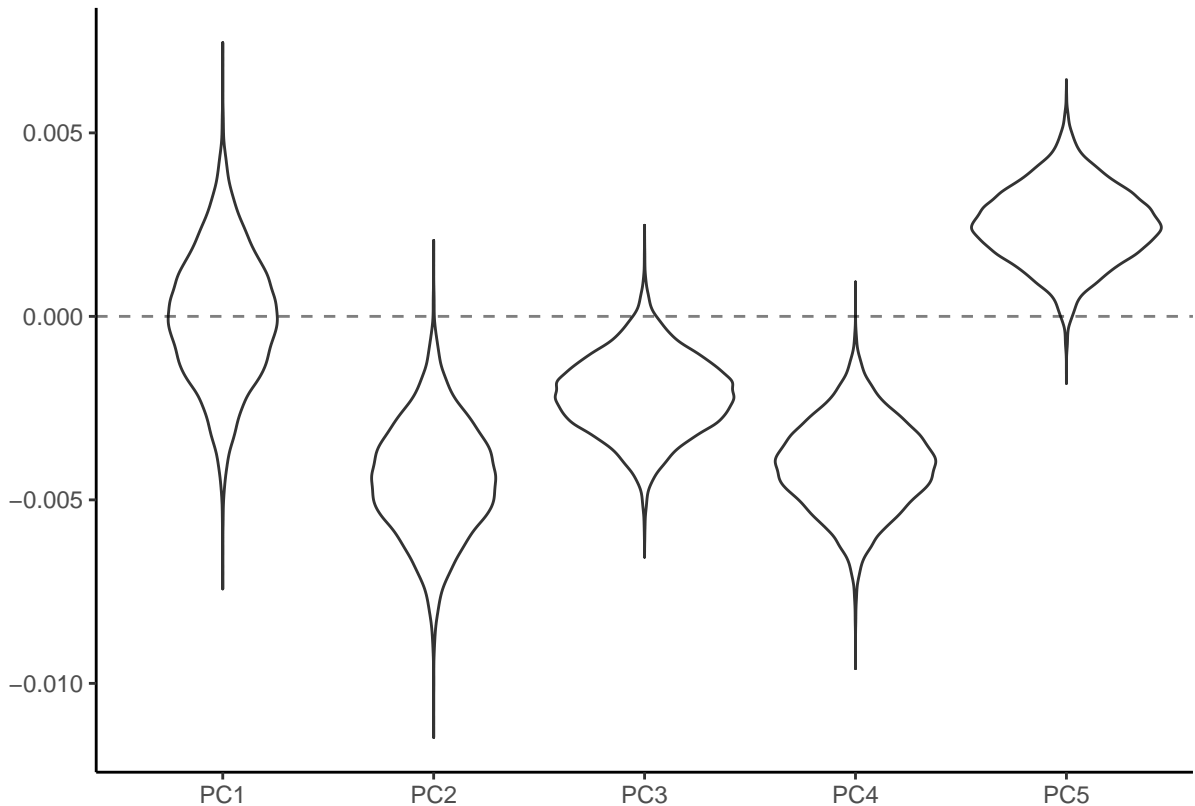


Figure 4: Full posterior distributions for θ values in Eq. (6). θ represent the contributions of principal components 1-5 to ϕ , the measure of maximum slope of the nonlinear equation (Eq. (1)).

4.0.5 Predictions of Thermal Sensitivity

We predicted thermal sensitivity at unsampled brook trout ~~habitat~~ throughout the study region using Eq. (1). Predicted β 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. 5). Among others, the Pendleton County, West Virginia, Nantahala National Forest in North Carolina, and the Great Smoky Mountains in North Carolina and Tennessee were predicted to have particularly stable stream temperatures. ~~A latitudinal gradient in slopes was also apparent here (Fig. 5), 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 sensitivity values, we found that 63% (1,367 of 2,175 sites) of preferred thermal habitat lies within protected areas.

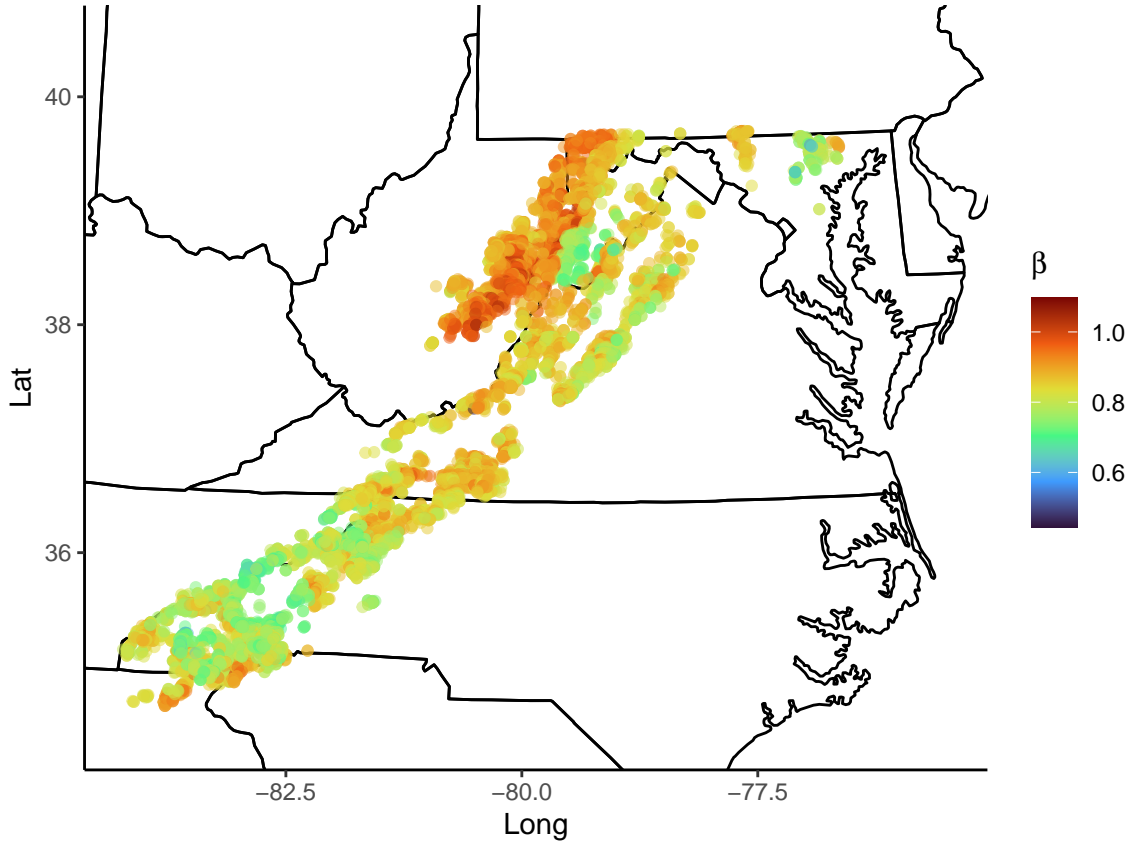


Figure 5: Predicted stream thermal stability at 8,660 sites of brook trout habitat in the southeastern USA. Thermal stability was predicted using posterior estimates from Eqs. (6) and (1), as well as spatially interpolated minimum and maximum stream temperatures.

5 Discussion

Our work represents one of the most geographically extensive analyses of thermal habitat for an aquatic species of conservation concern. The paired stream-air temperature data showed much thermal variation among 203 sites distributed along approximately 1,000 km of habitat, including some sites where stream temperatures were stable over time (weekly average $< 15^{\circ}\text{C}$) and others where stream temperatures warmed readily with increasing air temperatures. Such spatial thermal variability has been observed in other brook trout studies conducted over more geographically confined areas (Kanno et al., 2014; Trumbo et al., 2014). Given the thermal heterogeneity over space and upper thermal limits of brook trout ($22\text{--}24^{\circ}\text{C}$: Eaton et al., 1995; Hartman & Cox, 2008; Wehrly et al., 2007),

our study demonstrates that some current brook trout streams will likely maintain their ~~habitability~~ over a long period of time and may serve as climate refugia. Notably, principal components derived from landscape variables in the NHD explained a vast majority of variation in thermal sensitivity among sites, showing that readily available regional landscape data may be sufficient for describing why thermal heterogeneity exists in a region. Overall, our study highlights the importance of embracing spatial thermal variability for identifying thermal refugia and using this knowledge in maximizing the chance of sustaining coldwater species in a large landscape.

We found a latitudinal pattern of thermal refugia locations, where thermally resistant sites were clustered in the southern area (i.e., North Carolina and Tennessee) of the study region. More thermally resistant sites were characterized with cooler maximum average weekly temperatures, and this correlation between different thermal metrics provided further support for the robustness of our thermal refugia predictions. We reason that the latitudinal pattern of thermal sensitivity was due to spatial gradients of elevation in this study area, where elevation peaks in the southern area and decreases northward. Elevation has frequently been linked to thermal regimes that differ over space (Isaak et al., 2017; Maheu et al., 2016; Trumbo et al., 2014). Our finding of more thermally resistant sites in the southern area corroborates these results, as southerly sites have higher elevations than those in the north. ~~However~~, our finding contrasts with those of Flebbe et al. (2006), who did not account for spatially heterogeneous stream-air temperature relationships and projected a nearly complete eradication of southern Appalachian brook trout populations under future warming scenarios. Smaller clusters of thermal refugia were also identified in the northern area such as eastern West Virginia and eastern Maryland. Here, we ~~find~~ several of our sites with the least sensitive stream temperatures and logistic regression slopes < 0.5 . Overall, stream thermal sensitivity in our study area was typical of that reported by other authors (see Table 3 in Beaufort et al., 2020 for a comprehensive list), and average slope (0.85) fell within the range of those calculated for similar studies (0.3, Krider et al., 2013; 1.0, Webb, 1992). In general, thermal sensitivity of stream temperatures was spatially autocorrelated ~~resulting areas of thermal refuge~~, although this is not always the case in our data set and previous studies (Kanno et al., 2014; Snyder et al., 2015). ~~Nevertheless~~, our work is useful for identifying general clusters where thermal refugia mostly likely occur, to guide where conservation and restoration might be prioritized.

In addition to the conspicuous latitudinal pattern in locations of thermal refugia, the principal components of landscape variables ~~revealed complexities of thermal controls over space. Landscape influences on temperature were also corroborated by simple correlation of landscape metrics with thermal sensitivity.~~ In general, water temperature was more buffered against changes in air temperature



when streams had high **early summer flows**, low winter flows, and groundwater input. The degree of groundwater influence, represented by baseflow index, has consistently been identified as a determinant of thermal sensitivity (Beaufort et al., 2020; Briggs et al., 2018; Johnson et al., 2017; Kelleher et al., 2012; Tague et al., 2007). The importance of groundwater input at our sites can be inferred **ally** by inspecting the geographic locations of thermally stable sites. As with Ewin Run in West Virginia (Fig. 2), which is situated downstream of a noted spring, or Dumpling Spring Run in West Virginia, groundwater inflows appear to be responsible for these anomalies. In our study, metrics of water velocity (second and fourth axes of PCA) **explained spatial variation in thermal sensitivity slightly better than groundwater**. We surmise that water velocity may be **surrogate** for latent determinants of thermal sensitivity such as channel slope and morphology, which regulate solar radiation and surface-groundwater exchange (Caissie, 2006; Hauer et al., 2016). Urban landcover and soil permeability and wetness also explained thermal sensitivity, but to a more limited extent. Sediment, geology, and landcover may be linked to processes that affect stream temperature resiliency such as the water table depth and water retention in soils (Monk et al., 2013; Ryan, 1991; Snyder et al., 2015). As correlational evidence, the principal components of landscape variables cannot robustly identify ecological processes that generate spatial heterogeneity in stream temperature. Irrespective of the process uncertainties, these statistical relationships serve predicting thermal sensitivity for all stream segments potentially occupied by brook trout in the study area. **Previous research often used a limited number of landscape covariates to characterize spatial thermal variability** (Beaufort et al., 2020; Kelleher et al., 2012; Tague et al., 2007), and multivariate approaches should be considered more frequently, and especially for predictive purposes.

The spatial grain of our thermal sensitivity predictions was for NHD stream segments, given the landscape data availability for the large geographic extent of this study. However, thermal heterogeneity can occur within stream segments (Fullerton et al., 2017; Kalbus et al., 2006; Selker et al., 2006) and aquatic organisms may cue in highly localized areas of cold stream temperature to avoid unsuitably high temperatures in summer (Matthews & Berg, 1997; Sullivan et al., 2021). Additional research is warranted to investigate availability of spatially confined thermal refugia in stream segments that were predicted to respond **sensitively** to air temperatures, and this requires methods to characterize fine-scale thermal heterogeneity (e.g., fiber-optics cable, Selker et al., 2006) and habitat use by aquatic organisms (e.g., temperature tags, Hahlbeck et al., 2022). In the meantime, stream segments identified as thermal refugia in our study should be validated and this could be accomplished by deploying additional pairs of stream and air temperature loggers.

In conclusion, this study demonstrates that spatial thermal variability can be characterized

by readily available landscape variables for a large region. This knowledge is critical for managing coldwater species in a warming climate and identifying locations of climate refugia (Jones et al., 2014). Importantly, climate refugia should be defined and located based on stream thermal regimes ~~used~~ in conjunction with other key factors. Resistance and resiliency of aquatic populations under climate change depend not only on stream thermal regimes but also vulnerability of habitat to extreme wet (i.e., floods) and dry events (i.e., droughts) and habitat patch size and connectivity which affects post-disturbance recolonization and recovery of the populations (Ebersole et al., 2020). Such an integrative approach to identifying climate refugia is similarly important to strategizing landscape-level conservation of brook trout and other coldwater-dependent organisms in the southern and central Appalachian Mountains region.



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575 7 Appendix

576 7.1 Prior Distributions

577 For the logistic temperature model,

$$\epsilon_i \sim \text{normal}(\text{minWaterTemp}_i, 100),$$

$$\zeta_i \sim \text{normal}(\text{maxWaterTemp}_i, 100),$$

$$\kappa_i \sim \text{normal}(20, 100),$$

$$\sigma \sim \text{uniform}(0, 10),$$

$$\boldsymbol{\theta} \sim \text{normal}(0, 100),$$

$$\sigma_\phi \sim \text{uniform}(0, 10),$$

578 where minWaterTemp_i is the observed minimum water temperature ($^{\circ}\text{C}$) and maxWaterTemp_i is the
579 observed maximum water temperature ($^{\circ}\text{C}$) at site $i = 1, \dots, 203$.

7.2 Linear Temperature Model

For the linear regression, we removed observations where air temperatures were less than 0°C. In the linear model, we fit weekly mean water temperature T_W (°C) at site $i = 1, \dots, 203$ and week $t = 1, \dots, T$ as a function of weekly mean air temperature T_A (°C) with

$$T_{Wi,t} \sim \text{normal}(\alpha_i + \beta_i T_{Ai,t}, \sigma^2). \quad (5)$$

β_i is derived from the linear function

$$\beta_i \sim \text{normal}(\theta_1 + \theta_2 \text{PCA}_{1,i} + \theta_3 \text{PCA}_{2,i} + \theta_4 \text{PCA}_{3,i} + \theta_5 \text{PCA}_{4,i} + \theta_6 \text{PCA}_{5,i}, \sigma_\beta^2). \quad (6)$$

Priors for the linear model were

$$\alpha_i \sim \text{normal}(0, 1000), \sigma \sim \text{uniform}(0, 10), \boldsymbol{\theta} \sim \text{normal}(0, 100), \sigma_\beta \sim \text{uniform}(0, 10), \quad (7)$$

for site $i = 1, \dots, 203$.

We implemented and evaluated the linear model using the same methods described for the logistic model. All parameters converged at \hat{r} values of 1.1 or less. The model had an RMSE of 1.66 and a mean R^2 of 0.9. Posterior predictive checks showed little evidence for lack of fit, with mean Bayesian p-values for mean and standard deviation of 0.51 and 0.26. Linear regression slopes varied from 0.22 (95% HPDI: to) to 1.02 (95% HPDI: to), with an average slope of 0.72.

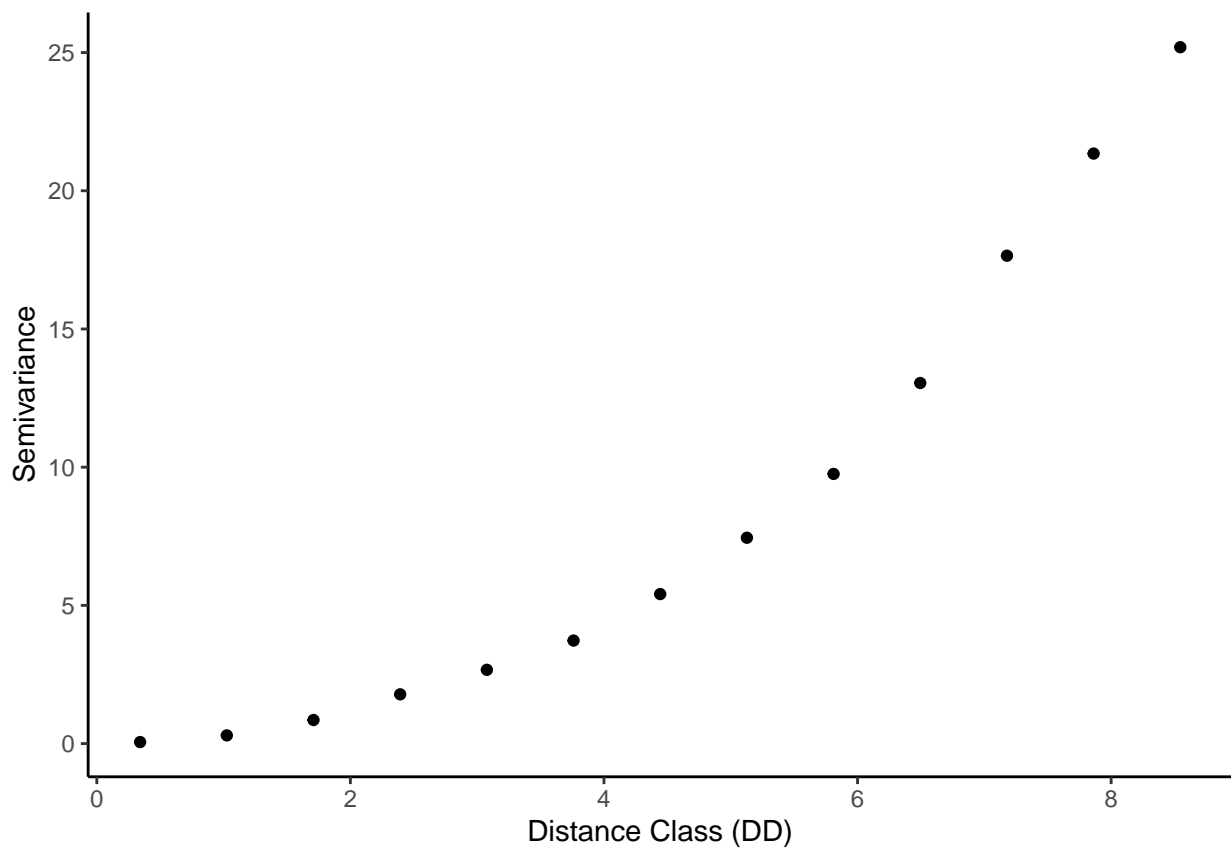


Figure S1: Semivariogram depicting spatial structure in thermal sensitivity at 203 sites. Slopes (model β s) are posterior means of the nonlinear model of weekly maximum temperatures.

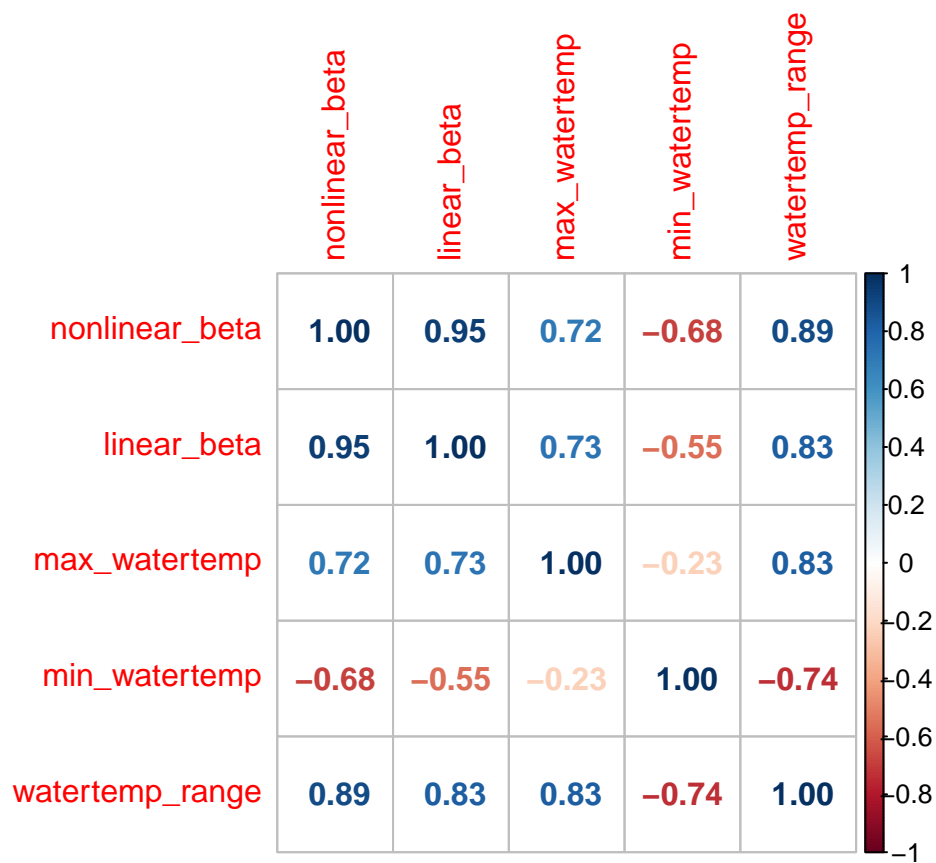
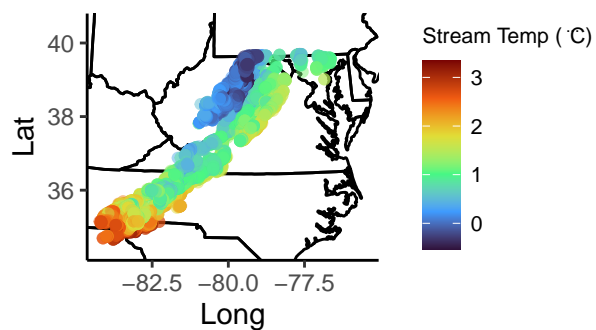


Figure S2: Pearson's correlations between nonlinear and linear model β and minimum, maximum, and range of weekly mean stream temperatures.

a)



b)

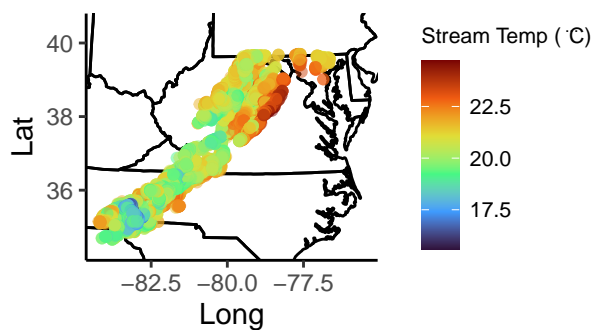


Figure S3: a) Minimum and b) maximum weekly stream temperatures at 8,660 sites of brook trout habitat. Sites were obtained through EcoSHEDS (www.usgs.gov/apps/ecosheds) and the Eastern Brook Trout Joint Venture (Eastern Brook Trout Joint Venture, 2006). Minimum and maximum stream temperatures were spatially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