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RESEARCH ARTICLE

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Landscape influences on thermal sensitivity and predicted spatial variability among brook trout streams in the southeastern USA

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Abstract

Warming water temperatures as a result of climate change pose a major threat to coldwater organisms. However, the rate of warming is not spatially uniform due to surface-ground-water interactions and stream and watershed characteristics. Coldwater habitats that are most resistant to warming serve as thermal refugia and identifying their locations is critical to regional aquatic conservation planning. We quantified the thermal sensitivity of 203 streams providing current and potential habitat for brook trout (*Salvelinus fontinalis*) across nearly 1000 linear km of their native range in the southern and central Appalachian Mountains region, USA, and characterized their spatial variability with landscape variables available in the National Hydrography Dataset. Using the Bayesian framework, we calculated the maximum slope of the logistic function relating paired weekly mean air temperature and stream temperature as an index of stream thermal sensitivity. Streams differed greatly in thermal sensitivity and those with more resistant water temperature regimes (i.e., thermal refugia) were consistently characterized by southerly latitudes and groundwater input. Landscape variables derived from a principal component analysis explained 16% of the variation in thermal sensitivity, indicating that the existing landscape variables were modestly successful in explaining spatial thermal heterogeneity. Using our model and spatial interpolation, we predicted thermal sensitivity at 8695 stream segments potentially suitable for brook trout in the study region. Thermal refugia were more common southward presumably due to higher elevations, but elsewhere they were also clustered at finer spatial scales. Our analysis informs prioritizing habitat conservation and restoration of this native salmonid and other aquatic organisms that depend on coldwater habitats in a warming world.

KEYWORDS

aquatic organisms, Bayesian, brook trout, climate refugia, landscape, Southeast USA, stream temperature, thermal sensitivity

1 | INTRODUCTION

Water temperature is a key component of lotic ecosystems, determining species composition, organismal metabolism, 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, challenges lie in locating climate refugia for coldwater organisms over a broad geographic extent. Stream temperature is chiefly influenced by radiative and convective heat fluxes with the atmosphere (Webb et al., 2008; Webb & Zhang, 1999). Nonetheless, generalized air temperature models are insufficient for predicting climate refugia and biotic responses to warming, as a multitude of atmospheric, hydraulic, and landscape characteristics and processes mediate the relationship between air and water temperatures (Caissie, 2006; Kirk & Rahel, 2022; Lisi et al., 2015; Poole & Berman, 2001). Physical models aim to overcome this by approximating solar radiation, air-water heat transfer, evapotranspiration, and groundwater input (Caissie, 2006; Kelleher et al., 2012; Lalot et al., 2015; Sinokrot & Stefan, 1993). However, these processes may differ spatially due to local hydrology, topography, and 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 (e.g., Crisp & Howson, 1982; Mackey & Berrie, 1991; Mohseni & Stefan, 1999; Stefan & Preud'homme, 1993; Zhu et al., 2018). 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°C) and high (>25°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 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 (Kelleher et al., 2012). The sensitivity of stream temperature relative to changes in air temperature can be used as an indicator of groundwater input, where more temporally stable stream temperature amid air temperature fluctuations signifies this buffered input (Beaufort et al., 2020; Hare et al., 2023; Kelleher et al., 2012). Thermal sensitivity and average water temperature are often strongly negatively correlated (Devine et al., 2021; Luce et al., 2014). As a result, thermal stability can provide an important signal in identifying thermal refuge for coldwater organisms.

Recently, more studies have aimed to elucidate trends in stream temperature and identify climate refugia. Most notably, NorWeST (Isaak et al., 2017) is a comprehensive project aimed at combining stream temperature observations across the western USA with the goal of interpreting and predicting climate impacts on streams and rivers. This work has identified potential climate refugia and predicted thermal habitat change across their study area (Isaak et al., 2015, 2016). Other works have been more limited in their geographic extent (i.e., individual US states or watersheds) and have focused on predicting spatial and temporal variation in water temperature at specific locations of interest, instead of identifying what factors determine the variation (Carlson et al., 2019; Carlson, Bowman, et al., 2017; Carlson, Taylor, et al., 2017; Kirk et al., 2022; Snyder et al., 2015). Key to broad-scale analyses is the growing body of publicly available national and regional watershed and hydrological data (e.g., US Environmental Protection Agency StreamCat or National Hydrography Dataset [NHD] in the USA), and few studies have been undertaken to explain or predict spatial variability using readily available watershed and hydrological data at broad spatial scales (Isaak et al., 2017; Mayer, 2012; Trumbo et al., 2014). 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, some studies of limited geographic extent have attributed spatial variability in thermal sensitivity to coarse-scale metrics such as riparian conditions, stream size, and geology (Beaufort et al., 2020; Chang & Psaris, 2013; Kirk et al., 2022; 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.

The brook trout (*Salvelinus fontinalis*) is 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 exceeding 22–24°C (Eaton et al., 1995; Hartman & Cox, 2008; Wehrly et al., 2007). Riverscapes characterized by cool stream temperatures allow brook trout 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; Snyder et al., 2015; Trumbo et al., 2014). However, these studies were limited in their geographical extent and we are not aware of previous work that 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 within the native range of brook trout.

We characterized landscape influences on stream thermal sensitivity across nearly 1000 km of the native range of brook trout in the southern and central Appalachian Mountains region, USA, using a multi-year dataset of paired stream and air temperature measurements. Located at their southernmost native range, the study area has experienced the greatest declines of brook trout populations (Hudy et al., 2008). Our study objectives were twofold. First, we used widely available landscape and hydrologic metrics to identify determinants of stream thermal sensitivity with a Bayesian hierarchical model of non-linear 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.

2 | METHODS

2.1 | Study area and dataset

We collected paired air and water temperature data from 203 stream segments in the southern and central Appalachian Mountains region of the USA (Figure 1). The mean elevation was 655.8 m (SD: 250.2 m) with a mean channel slope of 3.8% (SD: 4.1%) and a mean catchment area of 5.2 km^2 (SD: 8.1 km^2). The average Strahler stream order was 2. Stream segments in the southern Appalachians were generally

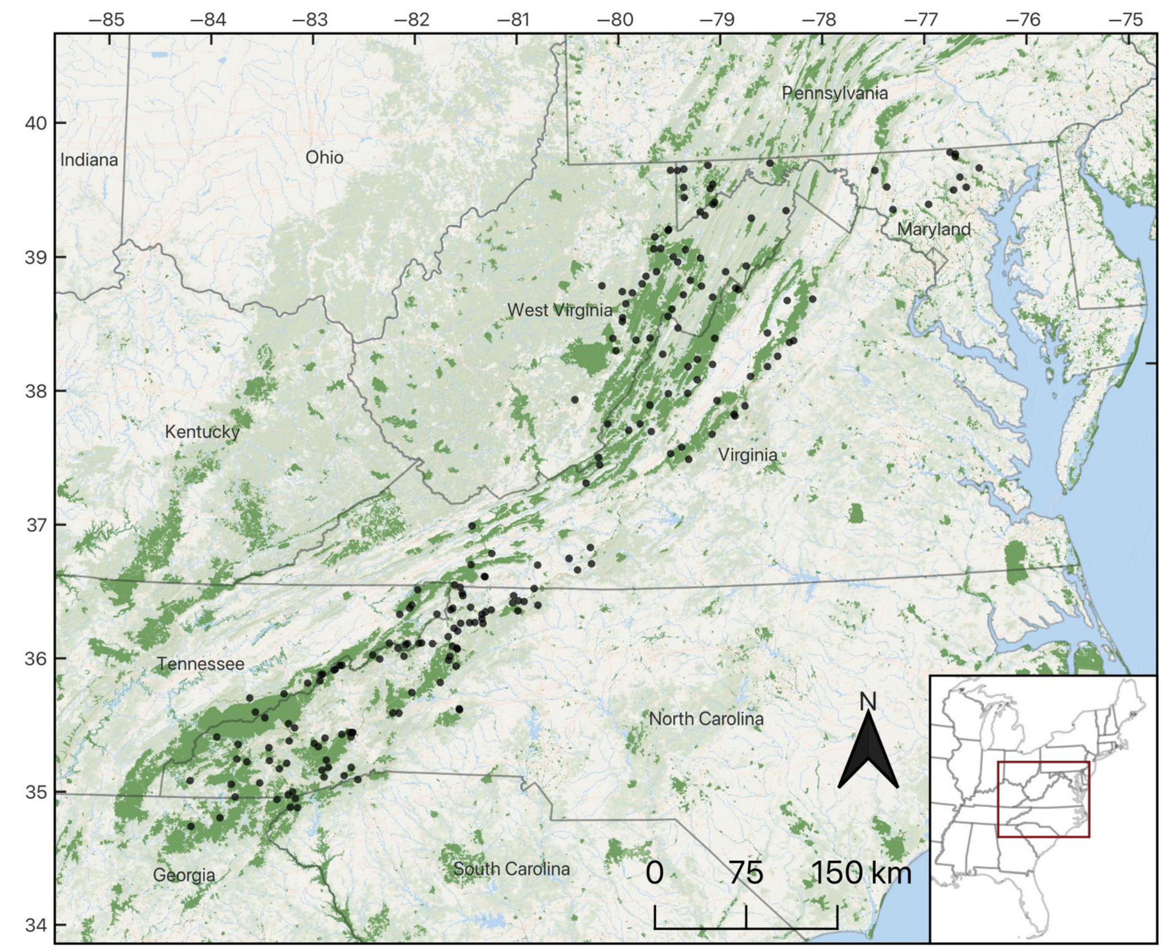

FIGURE 1 Locations of 203 stream segments where paired air and stream temperature data were collected from 2011 to 2015. Light green shading represents forested areas, and dark green shading indicates protected areas. The north and south halves of the study region were divided at 37.13° latitude. [Color figure can be viewed at wileyonlinelibrary.com]

situated at higher elevations than stream segments in the central Appalachians (mean 734 m vs. 563 m when divided at 37.13° latitude). Stream segments were located in randomly selected watersheds identified as capable of supporting populations of brook trout to represent a range of their habitats in the study region (Eastern Brook Trout Joint Venture, 2006; Li et al., 2016). Located at the downstream outlet of the watersheds, at each segment, a logger underwater was paired with a logger affixed to the bank or a tree. Stream and air temperatures were measured every 30 min between 2011 and 2015 using remote loggers (Onset Computer Corporation, Bourne, MA 02532). We summarized temperatures to weekly averages for data analysis.

A common drawback of studies of thermal sensitivity is that air temperatures are derived from model outputs or the closest meteorological station (Beaufort et al., 2020; Hare et al., 2021; Kelleher et al., 2012). This implies that trends in air temperatures used for analysis may not reflect the true trends influencing stream temperature at the local scale (Isaak et al., 2024; Kanno et al., 2014). Solar radiation and the influence of local topography have been shown to substantially 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 overcame this problem by using air temperatures measured in situ at the same locations where water temperatures were measured. Using these paired air and water temperature loggers, our study design allowed the consideration of highly local atmospheric influence on stream temperature.

Each segment was linked using a GIS to the NHD (NHDplus v2.1, U.S. Geological Survey, 2016) stream segment on which it was located. Using the NHDplus common identifier (COMID) code for each segment, we then accessed landscape metrics from the NHDplus and the US Environmental Protection Agency StreamCat database (Hill et al., 2016). The NHDplus includes stream segment data such as coordinates, elevation, slope, Strahler order, length, and drainage area, as well as metrics of monthly and annual flow and velocity. The StreamCat database includes metrics of landcover, geology, soil makeup, and climate at the watershed and stream segment catchment scale. Watersheds are defined here as the contributing area of land that drains to the outlet of the stream segment, while catchments are defined as portions of landscape that drains directly to a stream segment, excluding upstream contributions (Hill et al., 2016). A key to definitions for NHDplus and StreamCat variables can be found in Appendix A.3. Together, these two sources contributed 174 variables for each stream segment. Previous studies have identified groundwater, elevation, stream size, and channel slope as having a strong influence on stream thermal sensitivity (Beaufort et al., 2020; Chang & Psaris, 2013; Isaak et al., 2016; Mayer, 2012). Generally, shaded or headwater streams with small watersheds and groundwater inflows have the most stable thermal regimes. We considered additional metrics from the NHDplus and StreamCat to test an array of variables for their influences on thermal sensitivity and to improve predictive ability.

2.2 | Principal components analysis

We performed a Bayesian principal components analysis (PCA) of the 174 NHDplus and StreamCat predictors at 8695 stream segments of current and potential brook trout habitat identified in the USGS EcoSHEDS (www.usgs.gov/apps/ecosheds) by the Eastern Brook Trout Joint Venture (Eastern Brook Trout Joint Venture, 2006). The 203 segments with paired stream-air temperature measurements were included in the 8695 segments. We excluded segments with stream orders greater than five. Continuous variables were centered and scaled. We used a Bayesian PCA due to its ability to take missing values as 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 10 loadings by absolute value for the first five principle components (PCs; cumulative R^2: 0.60). Lastly, we extracted PCA scores for each of the 203 stream segments where temperature was measured.

2.3 | Hierarchical model

We used a Bayesian hierarchical logistic model to infer stream thermal sensitivity and the effects thereupon of local hydrology and landscapes. The regression slope at the inflection point of the function represents a first-order estimate of the relationship between air and water temperatures (Kelleher et al., 2012; Mohseni et al., 1998; Morrill et al., 2005). We omitted observations where water or air temperatures were missing. Following Mohseni et al. (1998), we fit weekly mean water temperature T_W (°C) at stream segment $i = 1,\ldots,203$ and week $n = 1,\ldots,N$ as a function of weekly mean air temperature T_A (°C) with:

$$T_{\mathrm{Wi,n}} \sim \mathrm{normal}\left(\alpha_i + \frac{\zeta_i - \alpha_i}{1 + e^{\phi_i(\kappa_i - T_{\mathrm{Ai,n}})}}, \sigma^2\right), \tag{1}$$

where ζ_i is the maximum weekly mean stream temperature (°C) at stream segment i, α_i is the minimum weekly mean stream temperature (°C), κ_i is the estimated air temperature at the inflection point of the function (°C), and ϕ_i is a measure of the slope of the function at the inflection point. Furthermore, ϕ_i was modeled as a random effect that varies with the PC scores:

$$\phi_i \sim \mathrm{normal}\left(\theta_0 + \theta_1 \mathrm{PC}_{1,i} + \theta_2 \mathrm{PC}_{2,i} + \theta_3 \mathrm{PC}_{3,i} + \theta_4 \mathrm{PC}_{4,i} + \theta_5 \mathrm{PC}_{5,i}, \sigma_\phi^2\right), \tag{2}$$

where θ represents the contribution of each PC to thermal sensitivity over space. The slope of the function at the inflection point (thermal sensitivity; β_i) at stream segment i is related to ϕ_i using the equation

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

We also estimated thermal sensitivity using linear regression (Appendix A.1), and inferences of thermal sensitivity were nearly identical to those of the nonlinear approach. Logistic regression slopes were also correlated with slopes from the linear regression ($r = 0.95$; Figure S2). We derived c to quantify the proportion of variance in thermal sensitivity among the 203 stream segments explained by landscape variables. c compares posterior samples of the residual variance in thermal sensitivity ($\hat{\sigma}^2_{\phi}$) to the variance in posterior samples of thermal sensitivity ($\hat{\phi}$):

$$c = 1 - \frac{\hat{\sigma}^2_{\phi}}{\mathrm{var}(\hat{\phi})}. \quad (4)$$

Values of c range between 0 and 1, with larger c values indicative of more variance explained by the principal components of landscape variables. In addition to evaluating variable loading in the PC and the posterior distribution of θ for that PC, we used Pearson correlation between segment-specific thermal sensitivity (β from Equation (3)) and landscape variables at each stream segment because some variables had loadings in more than a single PC. We chose landscape determinants of stream thermal sensitivity by identifying those variables that were both in the most significant PC loadings as defined by their posterior distributions and had the highest absolute correlation coefficients.

We conducted posterior predictive checks for the test statistics of mean and coefficient of variation to evaluate model performance (Conn et al., 2018). 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). Models that fit well result in Bayesian p-values that are not close to zero or one. We also evaluated the model using the root mean square error (RMSE) and R^2. Lower RMSE values indicate better model fit, and higher R^2 values indicate greater variance explained. We implemented the model with Markov Chain Monte Carlo sampling using JAGS with the "jagsUI" package in R (Kellner, 2024). We provide code in online supplements and report noninformative priors in Appendix A.2. After a burn-in period of 1000 samples, three chains were run until 5000 iterations were reached. We considered convergence as an $\hat{R}$ value of 1.1 or less (Gelman et al., 2004). We report posterior means as point estimates and 95% highest posterior density intervals (HPDIs) as estimates of uncertainty. We considered posterior distributions to be statistically significant when 95% HPDIs did not overlap with zero. We specified diffuse priors for all model parameters and used posterior mean predicted temperatures for subsequent analyses.

2.4 | Thermal sensitivity predictions and gap analysis

We predicted thermal sensitivity at unsampled brook trout habitat throughout the study region. In Section 2.2, we calculated principal components for 8695 stream segments of current and potential brook trout habitat. Using these principal components and posterior distributions for $\boldsymbol{\theta}$ from Equation (2) and (3), we calculated β_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 structure was modeled using an exponential covariance function based on pair-wise Euclidean distances.

Finally, we performed a gap analysis (Jennings, 2000) to evaluate the proportion of thermally buffered habitat that lies in protected areas and compared this to the proportion of total brook trout habitat that occupies 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 Protected Areas Database (Gap Analysis Project (GAP), 2022; Figure 1). We included protected areas with USGS Gap Analysis Project Status Codes 1–3. This included 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 NHDplus stream segments that were at least partially located in these protected areas. We then defined resistant thermal habitat as the lowest 25th percentile of predicted thermal sensitivity values. We calculated the percentage of resistant thermal habitat segments that were located on these stream segments within protected areas. Finally, we compared this percentage to that of all brook trout habitats located in stream segments within protected areas using a Chi-squared test.

3 | RESULTS

There was considerable thermal variability between stream segments. Average weekly air temperature across segments was 10.99°C (SD: 7.74°C) and ranged from −15.03 to 28.07°C. Average weekly water temperature across stream segments was 11.41°C (SD: 5.75°C) and ranged from 0 to 27.83°C. Some segments had thermally resistant water temperatures, but others were sensitive (Figure 2). Air and water temperatures generally were coolest in late January and early February, and peaked in mid-July. Minimum stream temperatures generally followed a latitudinal gradient, with the coolest minimums located in northern areas (Figure S1), however, maximum temperatures did not. Some of the coolest maximum stream temperatures were recorded at segments at southerly latitudes but located at higher elevations.

3.1 | Logistic model

The posterior predictive checks suggested little evidence of a lack of fit between model estimates and data. The mean Bayesian p-values for mean and standard deviation were 0.52 and 0.26. The nonlinear model had a mean R^2 of 0.91 and an RMSE of 1.73.

Thermal sensitivity differed greatly among the 203 segments, with evidence of thermal stability and thus thermal refugia. Logistic regression slopes (β) varied from 0.21 (95% HPDI: 0.18–0.25) to 1.24 (95% HPDI: 1.19–1.29), with an average slope of 0.85 (Figure 2).

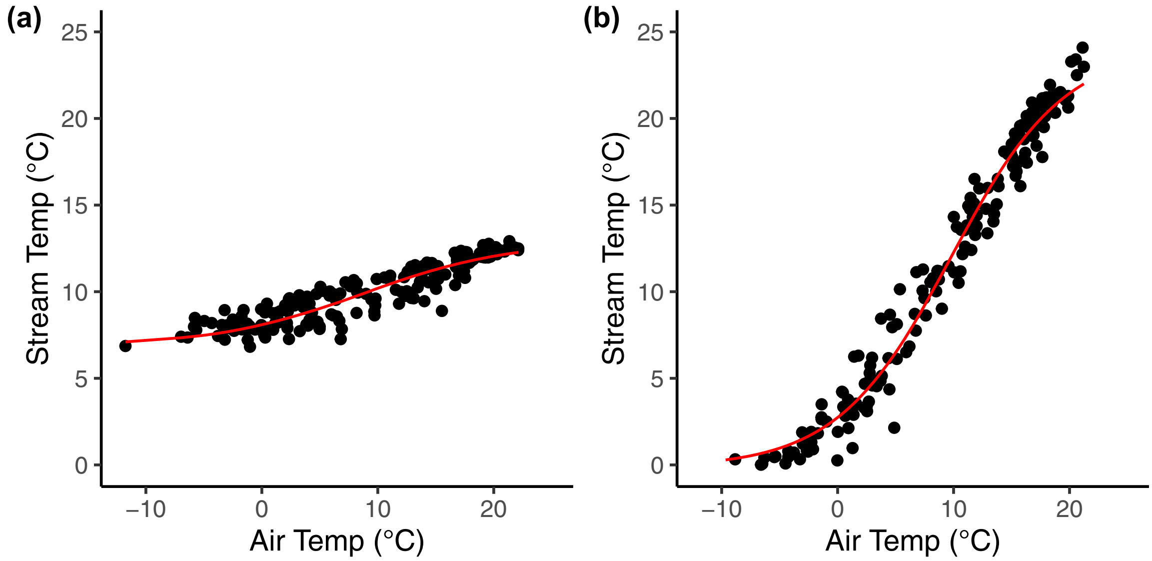

FIGURE 2 Logistic regression fits for (a) Ewin Run near Laurel Branch, WV, USA (low thermal sensitivity; $\beta = 0.21$) and (b) the Blackwater River near Cortland, WV, USA (high thermal sensitivity; $\beta = 1.24$). Black dots represent paired weekly average temperatures and red lines represent logistic regressions. [Color figure can be viewed at wileyonlinelibrary.com]

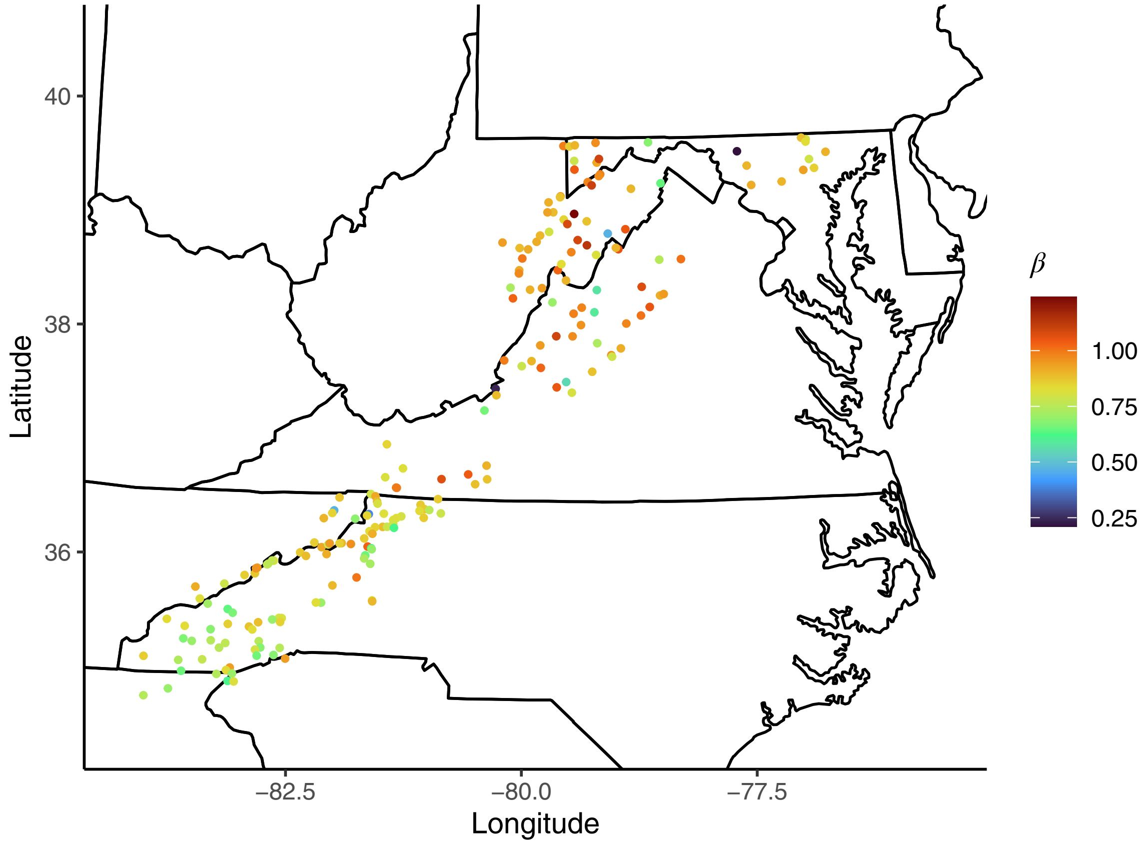

FIGURE 3 Air-water temperature slopes for each of the 203 measured stream segments. Slopes are β values from the nonlinear model of weekly mean water temperatures, with smaller β values equating to less sensitivity to changes in air temperatures (i.e., thermal refugia). [Color figure can be viewed at wileyonlinelibrary.com]

Smaller β values indicated less sensitivity in stream temperature to changes in air temperatures. These values were highly correlated with the minimum, maximum, and range of stream temperatures experienced among segments, indicating the robustness of this metric to evaluate spatial thermal heterogeneity (Figure S2). A latitudinal gradient in slopes was apparent, with less steep slopes (i.e., more resistant to changes in air temperature) generally present at southerly segments (Figure 3). Geographically confined pockets of thermal refugia were also present at northern latitudes. Thermal sensitivity was spatially structured, where nearer segments had more similar thermal sensitivity than farther segments (Figure 3).

3.2 | Landscape effects on thermal sensitivity

Spatial variability in thermal sensitivity was explained by landscape and hydrologic variables. In the PCA, the first five principal components explained 60% of the variance in these variables (Table 1) and 16% of spatial variance in thermal sensitivity (i.e., ϕ in Equation (1)). Spatial thermal sensitivity was not significantly explained by PC1 (metrics of monthly and annual stream flows), but significantly explained by PC2 (spring to summer water velocity), PC3 (coordinates, baseflow index, precipitation, and air temperature), PC4 (winter water velocity), and PC5 (landcover and geology) (Figure 4). Specifically, stream temperature was more buffered from (less sensitive to) air temperature fluctuations at stream segments characterized by low spring to summer water velocity (PC2: 95% HPDI = −0.007 to −0.0015), southern latitudes with higher baseflows (PC3: 95% HPDI = −0.004 to −0.0001), high winter velocity (PC4: 95% HPDI = −0.006 to −0.002), high soil permeability, and predominantly colluvial sediment and deciduous forest (PC5: 95% HPDI = 0.0004 to 0.004).

TABLE 1 Top five principal components (PCs) and percent variance explained (R^2).

PC1: 29.0%		PC2: 12.2%		PC3: 8.2%		PC4: 7.7%		PC5: 3.2%	
Variable	Loading	Variable	Loading	Variable	Loading	Variable	Loading	Variable	Loading
QC_11	−0.99	VC_07	−0.69	Lat	0.88	VC_01	0.76	WetIndexWs	0.54
QE_11	−0.99	VE_07	−0.68	Long	0.83	VE_01	0.76	PermWs	−0.52
QC_MA	−0.98	VC_05	−0.68	BFIWs	−0.76	VA_02	0.76	PermCat	−0.50
QC_10	−0.98	VE_05	−0.68	BFICat	−0.76	VA_01	0.72	PctUrbLo2016Ws	0.49
QC_06	−0.98	VA_06	−0.66	PrecipWs	−0.68	TmeanCat	0.65	PctColluvSedCat	−0.48
QE_MA	−0.98	VC_06	−0.66	PrecipCat	−0.67	VC_02	0.65	PctColluvSedWs	−0.48
QA_11	−0.98	VA_05	−0.66	TminWs	−0.64	VE_02	0.65	PctUrbOp2016Ws	0.45
QA_MA	−0.98	VA_07	−0.65	TminCat	−0.63	TmaxCat	0.65	PctUrbMd2016Ws	0.45
QE_05	−0.98	VE_06	−0.65	VC_02	0.61	TmaxWs	0.64	PctDecid2016Ws	−0.45
QE_04	−0.98	VE_11	−0.64	VE_02	0.61	TmeanWs	0.63	PctDecid2016Cat	−0.44

Note: The top 10 contributing variables for each principal component are listed based on their loadings. “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. Variable definitions are available in Appendix A.3, and further descriptions may be found in the NHDPlus User Guide and EPA StreamCat database.

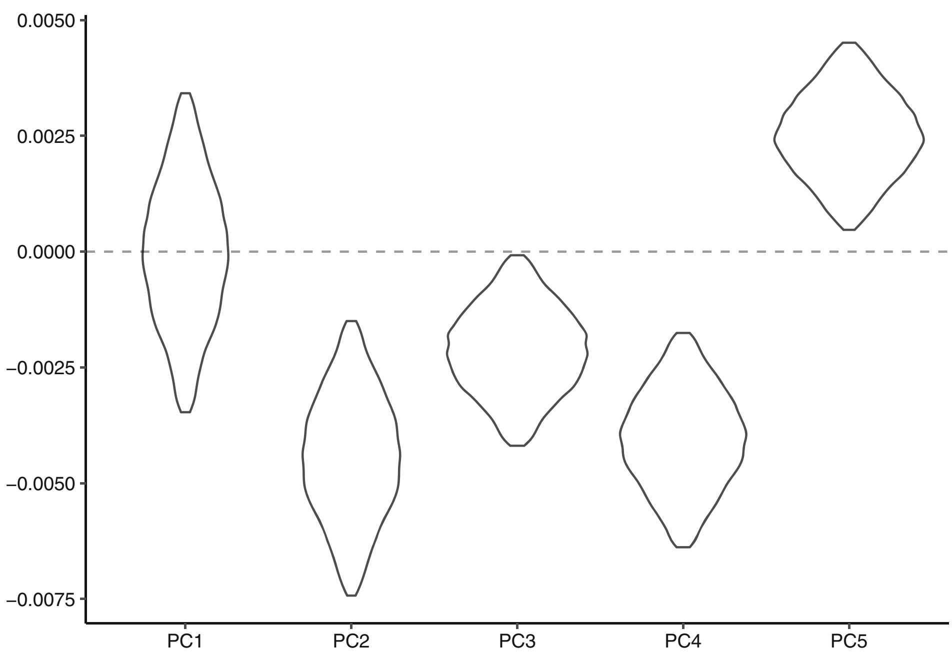

FIGURE 4 Violin plot trimmed at 95% highest posterior density intervals (HPDIs) for θ values, which represent the contributions of principal components 1–5 to ϕ, the measure of maximum slope of the nonlinear equation (Equation (1)). Significant distributions do not overlap with zero.

To complement the PCA, correlation analysis of individual variables showed that stream temperature was more buffered from air temperature fluctuations when baseflow index was high (Pearson $r = -0.45$), segments were located farther south ($r = 0.44$) and in smaller catchments ($r = 0.40$), and where segments were characterized with lower stream flows in March ($r = 0.40$). Taken together, latitude and baseflow index (i.e., a metric of groundwater) were consistently identified as determinants of spatial thermal sensitivity in the two analyses.

3.3 | Predictions of thermal sensitivity

Predicted thermal sensitivity varied greatly among unsampled stream segments, with values of β ranging from 0.45 (95% CI: 0.23–0.68) to 1.08 (95% CI: 0.93–1.23; Figure 5). Our predictions identified several areas most likely to serve as thermal refugia. 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. These pockets of potential climate refugia may also reflect the spatial interpolation techniques used in our predictions (Figure S1). Defining resistant thermal habitat as the lowest 25th percentile of predicted thermal sensitivity values, we found that 63% (1367 of 2175) of thermally resistant stream segments lay within protected areas. This is compared to 54% (4697 of 8695) of all segments evaluated. The proportion of protected thermally resistant segments was significantly greater than the proportion of overall habitat (Chi-squared $p < 0.001$).

4 | DISCUSSION

Our insights and predictions fit into a growing body of research leveraging large networks of water temperature loggers to inform conservation at regional and national scales (Isaak et al., 2017; Johnson et al., 2020; Mayer, 2012; Snyder et al., 2015). We build on this framework by combining these data with paired, in situ water temperature measurements and broad-scale landscape and hydrological data that allow predictions at unsampled locations and by expanding analyses of thermal sensitivity into the underrepresented southern and central Appalachian Mountains region of the southeastern USA. To our knowledge, our work represents one of the most geographically extensive analyses of thermal habitat for an aquatic species of

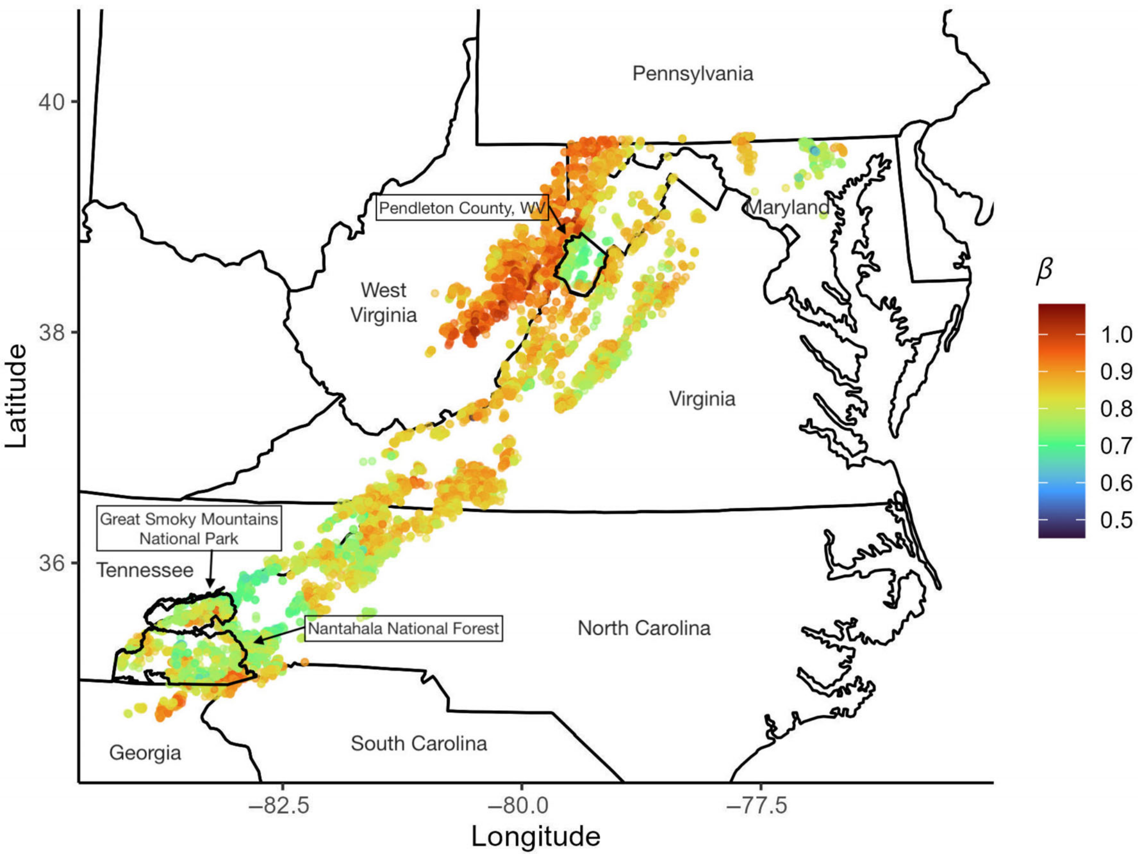

FIGURE 5 Predicted stream thermal sensitivity (β) at 8695 stream segments of brook trout habitat in the southern and central Appalachian Mountains region, USA. Thermal sensitivity was predicted using posterior estimates from Equations (6) and (1), as well as spatially interpolated minimum and maximum stream temperatures. Lower values of β indicate stream segments with less sensitive stream temperatures in relation to air temperature variation (i.e., thermal refugia). [Color figure can be viewed at wileyonlinelibrary.com]

conservation concern in the southeastern USA. The paired stream-air temperature data showed much thermal variation among 203 stream segments distributed along ca. 1000 km of habitat, including some segments where stream temperatures were stable over time (weekly average ~10°C; Figure 2) 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; Snyder et al., 2015; Trumbo et al., 2014). Given the thermal heterogeneity over space and upper thermal limits of brook trout (22–24°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 thermal habitat suitability over a long period of time and may serve as climate refugia. Principal components derived from landscape variables in the NHD explained only a moderate amount of variation in thermal sensitivity among stream segments, showing that coarse scale landscape data have limited abilities in describing why thermal heterogeneity exists among stream segments. Despite some limitations, our analysis revealed latitudinal patterns of thermal refugia locations and should serve as a basis in quantifying climate change impacts on aquatic species over a broad spatial extent. 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 stream segments were clustered in the southern area (i.e., North Carolina and Tennessee) of the study region. 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. Studies employing these generalized air temperature models often over-predict stream thermal and biotic responses to warming because water temperatures are often buffered by local landscape and hydrologic factors (Carlson et al., 2019; Carlson, Taylor, et al., 2017; Kirk & Rahel, 2022; Mitro et al., 2019). More thermally resistant stream segments were characterized with cooler maximum average weekly temperatures, and this correlation between different thermal metrics provided additional support for the robustness of our thermal refugia predictions. The latitudinal pattern of thermal sensitivity was likely due to spatial gradients of elevation in this study area, where elevation peaks in the southern area and decreases northward (elevation and latitude were negatively correlated: Spearman's $\rho = -0.4$). Elevation has previously been linked to thermal regimes that differ over space (Isaak et al., 2017; Maheu et al., 2016; Trumbo et al., 2014). The predominance of thermally resistant segments in the southern part of the brook trout range may also be explained by the legacy of anthropogenic impacts which have led to severe declines in the area (Hudy et al., 2008; Larson & Moore, 1985). Extant populations may already be confined to the most thermally resistant segments that represent a subset of their historical habitat range. In this sense, additional loss of brook trout habitat due to warming temperatures may occur more frequently at thermally sensitive stream segments located farther north in our study area. We also identified geographically confined clusters of thermal refugia in central Appalachian Mountains region areas such as eastern West Virginia and eastern Maryland. We located several segments with the least sensitive stream temperatures and logistic regression slopes <0.5. Overall, stream thermal sensitivity in our study area (mean slope = 0.85) was within the range reported by other authors (Beaufort et al., 2020; Krider et al., 2013; Webb, 1992). In general, the thermal sensitivity of stream temperatures was spatially autocorrelated, although this was not always the case in our dataset and previous studies (Kanno et al., 2014; Snyder et al., 2015). 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 latitudinal pattern in thermal refugia, the principal components of landscape variables and correlation analysis revealed complexities of thermal controls over space. In general, water temperature was more buffered against changes in air temperature where streams had low spring to summer velocities, smaller watersheds, 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; Carlson, Bowman, et al., 2017; Johnson et al., 2017; Kelleher et al., 2012; Tague et al., 2007). The importance of groundwater input at these segments can be inferred qualitatively by inspecting the geographic situations of thermally stable stream segments. As with Ewin Run in West Virginia (Figure 2), which is situated downstream of a noted spring, or Dumpling Spring Run in West Virginia, groundwater inflows appear to be responsible for their stability. In our study, metrics of water velocity (second and fourth axes of PCA) also explained spatial variation in thermal sensitivity. We surmise that water velocity may be a 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 resilience 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 contribute to predicting thermal sensitivity for all stream segments potentially occupied by brook trout in the study area. Previous research has used a limited number of landscape covariates to characterize spatial thermal variability (Beaufort et al., 2020; Carlson et al., 2019; Kelleher et al., 2012; Kirk et al., 2022; Tague et al., 2007), and multivariate approaches using large, publicly available datasets 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, landscape covariates at this scale were limited in their ability to explain spatial variation in thermal sensitivity ($c = 0.16$). This result was not surprising, and previous studies have similarly found that coarse-scale landscape data have limited abilities to explain spatial thermal heterogeneity (Chang & Psaris, 2013; Kelleher et al., 2012). Furthermore, 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 the availability of spatially confined thermal refugia in stream segments whose stream temperatures 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 temperature loggers.

In conclusion, this study demonstrates that some brook trout habitats will likely serve as thermal refugia in a changing climate, but that existing landscape data do not precisely predict their locations. This knowledge is critical for managing coldwater species in a warming climate and prioritizing conservation actions based on locations of climate refugia (Jones et al., 2014). Importantly, climate refugia should be defined and located based on stream thermal regimes 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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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are archived at sciencebase.gov. Code can be found online at github.com/gpvalentine/SE_Temp.

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SUPPORTING INFORMATION

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APPENDIX A

A.1 | Linear temperature model

For the linear regression, we omitted observations where air temperatures were less than 0°C. We then fit weekly mean water temperature T_W (° C) at site $i = 1,\ldots,203$ and week $n = 1,\ldots,N$ as a function of weekly mean air temperature T_A (°C) with

$$T_{Wi,n} \sim \text{normal}\left(\alpha_i + \beta_i T_{Ai,n}, \sigma^2\right); \tag{5}$$

where β_i is modeled as

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

Priors for the linear model were

$$\begin{aligned} \alpha_i &\sim \text{normal}(0, 1000), \\ \sigma &\sim \text{uniform}(0, 10), \\ \theta &\sim \text{normal}(0, 100), \\ \sigma_\beta &\sim \text{uniform}(0, 10), \end{aligned} \tag{7}$$

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

We implemented and evaluated the linear model using the same Bayesian framework 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: 0.19–0.24) to 1.02 (95% HPDI: 0.99–1.05), with an average slope of 0.72. For comparison, the nonlinear model had a mean R^2 of 0.91, an RMSE of 1.73, and an average slope of 0.85.

A.2 | Prior distributions

For the logistic temperature model,

$$\begin{aligned} \alpha_i &\sim \text{normal}(\text{minWaterTemp}_i, 100), \\ \zeta_i &\sim \text{normal}(\text{maxWaterTemp}_i, 100), \\ \kappa_i &\sim \text{normal}(20, 100), \\ \sigma &\sim \text{uniform}(0, 10), \\ \theta &\sim \text{normal}(0, 100), \\ \sigma_\phi &\sim \text{uniform}(0, 10), \end{aligned}$$

where minWaterTemp_i is the observed minimum water temperature (°C) and maxWaterTemp_i is the observed maximum water temperature (°C) at site $i = 1,\ldots,203$.

A.3 | Variable definitions

Hydrologic variables sourced from the USGS' NHDplus v2.1 (U.S. Geological Survey, 2016) follow the form YZ_XX. The first letter of the variable code (Y) represents the type of hydrologic variable, with "Q" representing flow predictions and "V" representing stream velocity predictions. The second letter of the variable code (Z) represents the origin of the hydrologic variable, with "A" representing cumulative runoff, "C" representing reference gauge regression, and "E" representing gauge flow. XX indicates the time period of record, with "MA" representing the mean annual statistic and numbers representing monthly statistics. Landscape variables sourced from the Environmental Protection Agency StreamCat database (Hill et al., 2016) are classified at either the watershed ("Ws") or catchment ("Cat") level. The NHDplus includes stream segment details such as coordinates, elevation, slope, Strahler order, length, and drainage area, as well as metrics of monthly and annual flow and velocity. The StreamCat database includes metrics of landcover, geology, soil makeup, and climate at the watershed and stream segment catchment scale. Watersheds are defined here as the contributing area of land that drains to the outlet of the stream segment, while catchments are defined as portions of landscape that drain directly to a stream segment, excluding upstream contributions (Hill et al., 2016). StreamCat abbreviations are as follows: BFI, baseflow index; PctColluvSed, % cover of colluviated sediment; PctDecid2016, % cover of deciduous landcover as measured from 2016 LandSat dataPctUrbLo2016, % cover of low-density urban landcover as measured from 2016 LandSat data; PctUrbMid2016, % cover of mid-density urban landcover as measured from 2016 LandSat data; PctUrbOp2016, % land cover of developed open space as measured from 2016 LandSat data; Perm, mean soil permeability; precip, precipitation; Tmax, maximum air temperature; Tmean, mean air temperature; Tmin, minimum air temperature; and WetIndex, soil wetness index. Further variable descriptions may be found in the NHDPlus User Guide and EPA StreamCat database metrics and definitions page.