Spatial asynchrony and cross-scale climate interactions in populations of a coldwater stream fish

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Abstract

Climate change affects populations over broad geographic ranges due to spatially auto-correlated abiotic conditions known as the Moran effect. However, populations do not always respond to broad-scale environmental changes synchronously across a landscape. We combined multiple datasets for a retrospective analysis of time-series count data (5–28 annual samples per segment) at 144 stream segments dispersed over nearly 1,000 linear kilometers of range to characterize the population structure and scale of spatial synchrony across the southern native range of a coldwater stream fish (brook trout, *Salvelinus fontinalis*), which is sensitive to stream temperature and flow variations. Spatial synchrony differed by life stage and geographic region: it was stronger in the juvenile life stage than in the adult life stage and in the northern sub-region than in the southern sub-region. Spatial synchrony of trout populations extended to 100–200 km but was much weaker than that of climate variables such as temperature, precipitation, and stream flow. Early life stage abundance changed over time due to annual variation in summer temperature and winter and spring stream flow conditions. Climate effects on abundance differed between sub-regions and among local populations within sub-regions, indicating multiple cross-scale interactions where climate interacted with local habitat to generate only a modest pattern of population synchrony over space. Overall, our analysis showed higher degrees of response heterogeneity of local populations to climate variation and consequently population asynchrony than previously shown based on analysis of individual, geographically restricted datasets. This response heterogeneity indicates that certain local segments characterized by population asynchrony and resistance to climate variation could represent unique populations of this iconic native coldwater fish that warrant targeted conservation. Advancing the conservation of this species can include actions that identify such priority populations and incorporate them into landscape-level conservation planning. Our approach is applicable to other widespread aquatic species sensitive to climate change.

KEYWORDS
Bayesian, brook trout, climate, portfolio effect, stream fish, synchrony, weather

1 | INTRODUCTION

Populations commonly experience shared temporal variation in abundance or demographic rates across a landscape. This spatial synchrony is often the strongest between nearby populations due to spatially autocorrelated abiotic conditions, known as the Moran effect (Moran, 1953; Royama, 1992) and biotic processes such as movement and predation (Koenig, 1999; Liebhold et al., 2004; Ranta et al., 1995). Spatially homogeneous population responses have been reported for distances near 1,000 km in some animals and plants (Koenig & Knops, 1998; Post & Forchhammer, 2002; Ranta et al., 1997). Such broad-scale responses are attributed to continental and regional climate patterns, which are key drivers of demographic rates (Koenig, 2002; Stenseth et al., 2002). The shared spatial scale of synchrony between climate drivers and population responses is typically regarded as a sign of the Moran effect (Koenig, 1999; Moran, 1953). As climate change accelerates, understanding the scale and drivers of spatial synchrony is critical to range-wide species conservation and management (Hansen et al., 2020).

Spatial synchrony as a result of climate is common in animals and plants, however local populations, even those in close geographic proximity, do not always display synchronous population trajectories (Herfindal et al., 2022; Sutcliffe et al., 1996). Heterogeneous population responses result not only because the magnitude of climate variation differs over space but also because the capacity to buffer against it differs locally. This cross-scale interaction between a broad-scale driver (e.g., climate) and local populations can occur due to the fine-scale spatial heterogeneity created by features such as local topography, microclimate variation, and surface-groundwater exchange (Fridley, 2009; McLaughlin et al., 2017). As a result, the strength of cross-scale interactions determines how synchronously a set of local populations respond to broad-scale drivers (Vendrametto Granzotti et al., 2022). A set of asynchronous population trajectories buffers species from range-wide declines (Heino et al., 1997; Roy et al., 2005), stabilizes populations over time at the regional scale (portfolio effect, Schindler et al., 2015, 2010; Wilcox et al., 2017), and increases socioeconomic resilience of resource use (e.g., hunting and angling, Cline et al., 2022). However, little empirical knowledge exists about how synchronous and asynchronous populations are situated across the landscape in widely distributed species.

Stream systems offer a unique opportunity for the study of macrosystems processes such as spatial synchrony and cross-scale interactions (McCluney et al., 2014). Streams are inherently characterized by spatial autocorrelation because downstream environmental patterns and processes such as temperature, biotic communities, and water chemistry are influenced by those upstream due to unidirectional flow (Isaak et al., 2017; Lloyd et al., 2005; Peterson et al., 2006). However, these processes do not typically prevail due to the spatial heterogeneity and network geometry created by stream confluences (Boddy et al., 2019; Frissell et al., 1986; Terui et al., 2018). Confluences represent geomorphic breaks where physical habitat characteristics such as stream size, temperature, and channel slope change abruptly, creating spatial heterogeneity in abiotic conditions (Benda et al., 2004) and demographic responses (Childress et al., 2019) across stream networks. Consequently, stream habitat is often characterized and classified by segment (i.e., from confluence to confluence, Frissell et al., 1986; U.S. Geological Survey, 2016). The stream segment is also the finest spatial grain at which stream habitat data are available at the national and continental scale (e.g., National Hydrography Dataset Plus [NHDPlus] dataset in the United States). Stream confluences are more numerous and average segment length is shorter in headwaters than farther downstream in stream networks (Wohl, 2017). Therefore, headwater stream networks contain habitat heterogeneity over relatively short physical distances, providing a template on which cross-scale interactions can occur.

Globally, headwater streams harbor a significant portion of remaining populations of coldwater fish such as trout and salmon, which are sensitive to variation in stream temperature and flow (Kovach et al., 2016). Temperature and flow are key abiotic drivers of population and community dynamics in stream biota (Maheu et al., 2016; Poff et al., 1997). Atmospheric air temperature, a key influence on and common surrogate for stream temperature, has increased steadily in the last century and is predicted to further increase (Pörtner et al., 2022). In the southeast United States, climate change is projected to increase precipitation and the occurrence of extreme flood events (Alipour et al., 2020; Ingram et al., 2013). Stream salmonids respond negatively to both high temperatures and high extremes of streamflow (Goode et al., 2013; Kanno et al., 2017; McCullough et al., 2009; Santiago et al., 2017). Climate effects on stream fish also vary by life stage and season. Early life stages of fish are sensitive to changes in streamflow. In particular, bed-scouring flows during incubation and emergence can wash away eggs and newly hatched individuals (Cattanéo et al., 2002; Kanno et al., 2015; Kovach et al., 2016; Schlosser, 1985). As stronger swimmers, adults are less sensitive to high streamflow, however, high water temperatures can result in increased stress and direct mortality, as well as impact spawn timing and reproductive success (Kovach et al., 2016; Pankhurst & King, 2010; Warren et al., 2012). As climate change amplifies these effects, stream fish populations at the rear edges of their distributions are particularly vulnerable (Hampe & Petit, 2005; Pregler et al., 2018).

We characterized the climate drivers of spatial synchrony by life stage (i.e., juvenile and adult) among populations of an iconic native coldwater fish (brook trout, *Salvelinus fontinalis*) across multiple spatial scales in the southern portion of their native range in the eastern United States. Remnant populations of this salmonid in the study region occur in small, isolated headwaters (Kazyak et al., 2022), which limit potential for dispersal among headwater networks. Furthermore, predation impacts from other species are low as many populations occur in allopatry (Hudy et al., 2008), precluding dispersal and predation as factors that might otherwise synchronize population trajectories over space. Brook trout are highly sensitive to climate drivers such as stream temperature and flow (Kanno et al., 2017; Roghair et al., 2002; Warren et al., 2012; Xu et al., 2010).

Consequently, this species provides an opportunity to investigate population synchrony attributable mainly to climate variation.

Our study aims were threefold. First, we quantified the scale and strength of spatial synchrony among brook trout populations and compared it with those of spatial synchrony in climate variables (i.e., temperature, precipitation, and streamflow). We hypothesized that patterns of spatial synchrony would be similar between the climate variables and trout populations, if climate variables exerted a strong and spatially homogeneous effect on population trajectories (Koenig, 1999; Levin, 1992; Wiens, 1989). Second, we tested whether spatial synchrony was explained by a set of seasonal climate variables and whether the importance of seasonal climate variables differed between and within northern and southern sub-regions. Because we studied a sensitive coldwater species at its southern range limit, we predicted that temperature would be a stronger driver of synchrony in southern populations compared to northern populations (Maitland & Latzka, 2022). Furthermore, we predicted that winter and spring stream flow would be a stronger driver of synchrony in the young-of-the-year (YOY) (juvenile) stage versus adult stage of this fall spawner due to the diminished ability to withstand bed-scouring high flows of the younger stage (Kanno et al., 2016; Kovach et al., 2016). Third, we quantified stream segment-specific population trajectories relative to the overall trajectory across segments to characterize how synchronous and asynchronous populations are distributed in the landscape. Asynchronous populations that deviate from the overall trajectory hold conservation value when asynchrony is due to population resiliency to environmental changes or habitat serving as climate refuge (Hilborn et al., 2003; Schindler et al., 2010, 2015). To address these aims, we assembled time-series abundance data at 144 stream segments spanning nearly 1,000 linear kilometers of brook trout range across the southern Appalachian Mountains of the eastern United States.

2 | METHODS

2.1 | Study species

Brook trout are native to eastern North America, distributed from the Appalachian Mountains in northern Georgia to the coasts of Newfoundland and Labrador in Canada and inland as far as Minnesota in the United States. They are culturally and economically important, designated as the state fish of nine US states. Brook trout are among the most popular freshwater sportfish in the United States (American Sportfishing Association & Sport Fish Restoration, 2021). They spawn in fall, and their eggs overwinter in streambed nests ("redds") to hatch in early spring (Hazzard, 1932). They can reach maturity as early as 1 year of age, and seldom live longer than 3 years in their southern range (Donald & Alger, 1989; Larson & Moore, 1985; Meyer et al., 2006). Brook trout are highly sensitive to water temperature and cannot withstand prolonged temperatures above 22–24°C (Eaton et al., 1995; Wehrly et al., 2007) and spawning is deleteriously affected by high summer and fall temperatures (Warren et al., 2012).

Redds are scoured and young brook trout are swept away by high stream flows during winter and spring months (Kanno et al., 2015). Because of their high environmental specificity, brook trout are often considered an aquatic indicator species. Due to anthropogenic activities, they have experienced large declines, particularly in their southern native range (Hudy et al., 2008).

We consider that if spatial synchrony occurs in brook trout, it is most likely due to the Moran effect rather than dispersal dynamics because stream populations are typically isolated by unsuitable riverine habitat downstream and physical barriers such as waterfalls and road crossings. Kanno et al. (2016) found that seasonal air temperature and precipitation led to spatial synchrony in YOY brook trout, but not in adults, at scales of up to 170 km. Zorn and Nuhfer (2007) found correlations between brook trout density and spring discharge in Michigan rivers. Spatial synchrony due to the Moran effect has been described in other stream-dwelling salmonids (Cattanéo et al., 2003; Lobón-Cerviá, 2007; Zorn & Nuhfer, 2007). Despite these indications of synchrony in brook trout, prior work has been limited to single datasets (i.e., Kanno et al., 2016; Zorn & Nuhfer, 2007), and no study has attempted a broad-scale analysis of spatial synchrony in this species.

2.2 | Study area and dataset

Our study area comprised the far southern and eastern native range of brook trout in the United States, from the southern Appalachian Mountains in Georgia to Maryland (Figure 1). We compiled a dataset with over 200,000 brook trout individuals in 144 stream segments
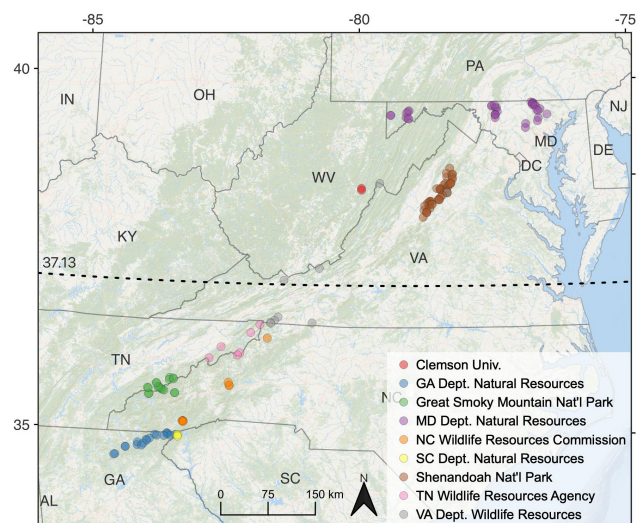
FIGURE 1 Map of 144 study stream segments where electrofishing data were available (5–28 annual samples per segment). Dotted line (37.13° latitude) divides north and south sub-regions. Dot colors represent the agencies/groups that collected the data. GA, Georgia; MD, Maryland; NC, North Carolina; SC, South Carolina; TN, Tennessee; VA, Virginia. Basemap: Environmental Systems Research Institute (ESRI).

from nine state, federal, and private sources between 1982 and 2015 (Table S1). All stream segments had ≥5 years of data during this time period (range: 5–28 years of data). Data consisted of individual trout measurements, sampling occasion data, and stream segment data. Individual trout measurements included total length (mm) and weight (g). Sampling occasion data included date and number of electrofishing passes. Stream segment data included National Hydrography Dataset Plus (NHDPlus) stream segment common identifier (COMID), coordinates (decimal degrees), elevation (m), and length and median width (m). Study segments were located in headwater streams with a mean wetted width of 5.1 m (Table 1). We divided the northern and southern sub-regions at 37.13° latitude— that of the New River Valley in Virginia, which aligns with a major shift in genetic patterns of this species (Kazyak et al., 2022). The mean elevation was higher and channel slope was steeper in the southern versus northern sub-region (905.5 m vs. 461.9 m in elevation; 6.6% vs. 3.6% in slope). The mean maximum summer (June–September) air temperature was higher in the southern sub-region (25.7°C) than in the northern sub-region (24.6°C).

All brook trout data were collected by backpack electrofishing in wadeable streams (mean site length: 128 m). A combination of single- and multi-pass sampling methods (single: 32%, multi: 68%) was employed following standardized sampling protocols for the southern USA region (SDAFS Trout Committee, 1992). In multi-pass sampling, fish were removed from the stream in successive passes in temporarily blocked stream reaches to estimate capture probability and thus population size. Sampling boundaries were defined by block nets or cobble dams which served as barriers for fish movement. Depending on stream width, one to three backpack electrofishing units were used. A majority of sampling occurred in June–October. Samples taken in lakes and ponds, as well as observations of hatchery-born fish, were excluded. We also excluded segments with less than 10% brook trout in fish assemblages. YOY brook trout were defined as those ≤90 mm total length, and adults were defined as those >90 mm total length. We summarized the data to counts by life stage, sampling occasion, and electrofishing pass.

To spatially match trout data with predictors, we pooled trout count and surface area surveyed across sites when multiple sites were surveyed annually in an NHDPlus stream segment (a length of a stream delineated by either its beginning and a confluence, or by two confluences (U.S. Geological Survey, 2016); average segment length = 3.3 km). Brook trout in headwaters typically remain within several hundred meters of their hatching locations (Hudy et al., 2010; Rodríguez, 2002). Thus, pooling count data by stream segment allowed us to account for dispersal within segments and demographic independence among segments. On average, 34% of stream segments contained more than one collection site.

2.3 | Correlogram analysis

We quantified the magnitude and scale of spatial synchrony in YOY and adult brook trout using the nonparametric spatial covariance function Sncf in the "ncf" package for R (Bjørnstad, 2022; Bjørnstad & Falck, 2001; R Core Team, 2022). We then extracted estimates of both initial and average spatial correlation and the Euclidean distances to which spatial covariance extends. We visually represented synchrony using spline correlograms, which portray the spatial decay in pairwise correlation between segments. The scale of synchrony (correlation length) can be interpreted as the distance at which the confidence envelope of the spline function is significantly higher than the sample average (x-axis, Bjørnstad & Falck, 2001). We selected 72 stream segments with 5 years or more multi-pass electrofishing data between 1995 and 2015. We further removed segments where the focal life stage was never collected, resulting in 70 segments for YOY and 68 segments for adults. We conducted the correlogram analysis of the two life stages at both the regional and sub-regional levels. We calculated 95% CIs for the correlograms using the bootstrap algorithm in the "ncf" package. We truncated pairwise Euclidean lag distances to 2/3 the total distance observed following Fletcher et al. (2018). Abundances at each sample were estimated using the removal function in the "FSA" package for

TABLE 1 Summary statistics for segment characteristics and climate variables (1980–2015) by sub-region.

	North		South	
	Mean	SD	Mean	SD
Channel slope (%)	3.6	2.9	6.6	4.7
Length (km)	3.7	2.9	2.8	1.7
Catchment area (km^2)	6.9	9.1	3.6	3.1
Elevation (m)	461.9	212.4	905.5	207.7
Stream order	2.0	1.0	1.0	1.0
Wetted width (m)	5.1	3.1	5.1	2.4
Max summer temperature (°C)	24.6	2.5	25.7	1.8
Max 0.9Q winter stream flow (cfs)	61.5	226.6	56.9	144.0
Max 0.9Q spring stream flow (cfs)	105.0	369.9	56.0	134.8

Note: Summer: June–September Winter: December–February. Spring: March–May. *Sources*: Oak Ridge National Labs DAYMET, US Geological Survey NHDPlus.

R (Ogle et al., 2022), which uses electrofishing depletion counts to estimate abundance. Using these predicted abundances, we calculated the natural log of average density (fish/1000 m^2) at each stream segment and year. We imputed missing data when necessary for the analyses and show in Appendix S10.1 that the results were robust to this imputation.

We compared the magnitude and scale of spatial synchrony in brook trout abundance to those of mean summer water and air temperature and winter streamflow and precipitation (2016; Kanno et al., 2015). We obtained observed air and water temperatures at 30-min intervals (Li et al., 2016). They were measured using a network of 204 paired temperature loggers located in brook trout streams in the southeast United States from 2011 to 2015 (Figure S2). Although atmospheric air temperature is not always an appropriate surrogate for stream temperature (Kirk & Rahel, 2022), these air and water temperatures were highly correlated (mean $r = 0.95$, Pearson). We summarized these temperatures to annual summer (June–September) means because spatial variation in stream water temperatures is greatest during summer base flow condition (Beauchene et al., 2014). Monthly streamflow estimates were obtained from the NHDPlus V2 (U.S. Geological Survey, 2016) for the stream segments used in the correlogram analysis of trout populations. We summarized these estimates to annual winter (December–February) means. Hourly observed winter precipitation (2008–2014) data were obtained for 51 NOAA NCEI measurement sites within the geographic extent of the trout data (Figure S3, National Oceanic and Atmospheric Administration, & National Centers for Environmental Information, 2022) and summarized to annual winter (December–February) totals. As with the brook trout data, we used the nonparametric spatial covariance function Sncf in the "ncf" package to quantify the magnitude and scale of spatial synchrony in these climate variables.

2.4 | Hierarchical model

We developed two Bayesian hierarchical models to quantify the effects of climate variables on synchronous dynamics of brook trout populations by life stage (Berliner, 1996; Wikle et al., 1998). For each, we developed an N-mixture model (Royle, 2004) using a removal mechanism coupled with a log linear process model. In the first, hereafter the climate effects model, we inferred brook trout count as a function of summer temperature and winter and spring streamflow in the season preceding sampling. We elected to model brook trout abundance as a function of density-independent climate variables but not density-dependent factors because the former have consistently overwhelmed the latter in studies of brook trout population dynamics (Kanno et al., 2016; Letcher et al., 2015; Sweka & Wagner, 2022). This model employed both single- and multi-pass electrofishing abundance data from 144 stream segments collected between 1982 and 2015. In the second, hereafter the random effects model, we inferred brook trout count as a function of a temporal random effect and a spatiotemporal random effect. This model employed abundance data from 102 stream segments sampled with

multi-pass electrofishing techniques between 1988 and 2015. We elected to use separate models for climate and random effects after encountering convergence issues using a single, combined model (however, the simulation in Appendix S10.2 demonstrates that parameters are identifiable in such a model). Models lacking random effects overestimate the precision (i.e., underestimate 95% credible intervals) of regression coefficients such as climate effects in our study, but their point estimates (i.e., posterior means) are much less affected (Schaub & Kéry, 2012). Therefore, our analysis should provide reliable inferences on the relative importance of temperature and flow effects and their spatial variation on trout abundance.

Adapting the standard N-mixture model to allow our removal sampling data at segment $i = 1, \ldots, N$, and year $t = 1, \ldots, T$ for each of $j = 1, \ldots, 3$ electrofishing passes, we specified the data model

$$y_{i,j,t} \sim \begin{cases} \text{binomial}(N_{i,t,p_s}) & \text{if } j = 1 \\ \text{binomial}\left(N_{i,t} - \sum_1^{j-1} y_{i,j,t}, p_s\right) & \text{if } j > 1, \end{cases} \quad (1)$$

where $y_{i,j,t}$ is observed count of YOY or adult brook trout at segment i, pass j, and year t. We denote $N_{i,t}$ as the predicted count of the given life stage in year t at segment i. We modeled abundance separately for passes $j > 1$ because there are $\sum_1^{j-1} y_{i,j,t}$ fewer individuals in the sampling area after removing them in each pass. The term p_s represents the capture probability of individuals for data source $s = 1, \ldots, S$ (Figure S4). We used informative priors for p such that $p \sim \text{beta}(0.5, 0.1)$ for YOY and $p \sim \text{beta}(0.65, 0.1)$ for adults, based on their differences in capture probability (Kanno et al., 2015). We allowed capture probability to vary by agency because sampling crew capture is often a large source of variation in sampling efficiency (Hughes et al., 2002; Kimmel & Argent, 2006; Meador, 2005). We modeled abundance in each stream segment and year conditional on local density $\lambda_{i,t}$ (fish/1000 m^2) as

$$N_{i,t} \sim \text{Poisson}\left(\frac{a_{i,t}}{1000} \lambda_{i,t}\right), \quad (2)$$

where $a_{i,t}$ is the sum of site areas (length × median wetted width) sampled for stream segment i and year t.

For the climate effects model, local abundance was represented as a function of three climate covariates. Daily maximum air temperature predictions for each stream segment were obtained from the DAYMET model (Thornton et al., 1997, 2014, 2021) using the "daymetr" package in R (Hufkens et al., 2018). Monthly flow percentile predictions for each stream segment were obtained from the NHDPlus V2 (U.S. Geological Survey, 2016). We summarized summer high temperature as the mean of daily maximum predictions between June and September in year $t - 1$. We used previous year summer temperatures to account for temporal discrepancies between trout sampling and temperature measurements. We summarized winter (December–February) and spring (March–May) high stream flows as the maximum of monthly 90th percentile flow estimates. All climate covariates were centered and scaled by stream segment. Brook trout density was modeled as a function of these covariates $x_{i,t}$ using the log-link function

$$\log(\lambda_{i,t}) = \omega_i + \mathbf{x}'_{i,t}\boldsymbol{\beta}_i, \tag{3}$$

where ω_i represents average log density at segment i when climate variables are set at their mean and $\boldsymbol{\beta}_i$ represents a vector of segment-specific climate covariate effects. Priors on ω_i and $\boldsymbol{\beta}_i$ were non-informative: $\omega_i \sim \text{normal}(0, 1000)$ and $\boldsymbol{\beta}_i \sim \text{normal}\left(\boldsymbol{\mu}_\beta, \boldsymbol{\sigma}_\beta^2\right)$ where $\boldsymbol{\mu}_\beta \sim \text{normal}(0, 100)$ and $\boldsymbol{\sigma}_\beta \sim \text{uniform}(0, 10)$. As a random effect, $\boldsymbol{\beta}_i$ allows the estimation of both local (stream segment specific) and overall covariate effects.

The synchronizing effects of the climate covariates in Equation (3) can be estimated from the variances of the covariate coefficients ($\boldsymbol{\sigma}_\beta^2$). A coefficient with low variance (i.e., similar effects on different populations) has a strong synchronizing effect. A covariate with a high variance (differing effects on different populations) has a weak synchronizing effect.

For the random effects model, local abundance was represented as a function of segment-specific intercept and two random effects:

$$\log(\lambda_{i,t}) = \omega_i + \epsilon_t + \gamma_{i,t}, \tag{4}$$

where ω_i represents average log density at segment i with the diffuse normal prior $\omega_i \sim \text{normal}(0, 1000)$. The terms ϵ_t and $\gamma_{i,t}$ represent temporally and spatiotemporally structured random effects, respectively. The random effects are assumed to be independent with distributions $\epsilon_t \sim \text{normal}\left(0, \sigma_\epsilon^2\right)$, $\sigma_\epsilon \sim \text{uniform}(0, 10)$, $\gamma_{i,t} \sim \text{normal}\left(0, \sigma_{\gamma,i}^2\right)$, and $\sigma_{\gamma,i} \sim \text{uniform}(0, 10)$. The ϵ_t term represents the between-year variation in density that is synchronous to all segments, and the $\gamma_{i,t}$ term represents the variation that is segment specific (i.e., asynchronous).

Following Grosbois et al. (2009) and Lahoz-Monfort et al. (2011), we used posterior samples of the estimated variances of the two random effect terms to derive a segment-specific intraclass correlation coefficient (ICC):

$$\text{ICC}_i = \frac{\hat{\sigma}_\epsilon^2}{\hat{\sigma}_\epsilon^2 + \hat{\sigma}_{\gamma,i}^2}. \tag{5}$$

The ICC serves as a measure of synchrony of the local population in segment i relative to the temporal variation averaged across all segments. This metric ranges from 0 to 1, with values closer to 1 indicating that the given segment was synchronous with the averaged temporal variation and 0 indicative of asynchrony. We created semivariograms of YOY and adult ICC values to check for spatial structure in synchrony.

We tested for the presence of a portfolio of population responses by comparing segment-specific interannual variability in observed abundance to that of all segments following Schindler et al. (2010). We calculated the coefficient of variation in pass 1 YOY abundance for each segment, as well as in the average of pass 1 YOY abundance for all segments. A smaller coefficient of variation across all segments than in individual segments demonstrates a portfolio effect.

We fit a total of 12 models: One random effects and one climate effects model each for YOY and adults at the regional scale

fit to all stream segments (hereafter the "regional" models), as well as the same set of models in the northern and southern halves of the study region, hereafter the "sub-regional" models. 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 "Code Availability Statement". After a burn-in period of 5,000 samples for the climate effects models and 20,000 for random effects models, three chains were run without thinning until 25,000 and 50,000 samples were obtained, respectively. All chains converged, as visually evaluated using trace plots. To evaluate the performance of our models, we conducted posterior predictive checks for the test statistics of mean and coefficient of variation of pass 1 abundance. 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, with values closer to .5 indicative of adequate fit. We report posterior means as point estimates and 95% highest posterior density intervals (HPDIs) as estimates of uncertainty. Effects were considered significant if their 95% HPDIs did not overlap 0.

3 | RESULTS

3.1 | Correlogram analysis

The average scale and magnitude of spatial synchrony in both YOY and adult brook trout was low compared with those of a suite of climate variables (Figure 2). Correlation lengths measured using the 95% confidence envelope of the spline correlogram were 84 km in YOY and 70 km in adult brook trout. Point estimates for the scale of synchrony were roughly 100 km for YOY and 200 km for adults. Summer air and water temperature and winter streamflow and precipitation were synchronous to scales of 400 km or more. There was little overlap in the 95% confidence interval (CI) of initial pairwise correlation between trout density and abiotic variables. Average pairwise correlations in YOY and adult brook trout were 0.07 and 0.05, respectively, and those of the climate variables ranged from 0.51 to 0.64. The average magnitude of synchrony was greater in the northern than in the southern sub-region for both life stages (Figure 3). Initial pairwise correlation was considerably higher in the northern sub-region for adults (mean = 0.31; 95% CI = 0.16–0.46 vs. mean = 0.06; 95% CI = −0.1 to 0.2 for the southern sub-region). The scale of synchrony did not differ greatly between sub-regions.
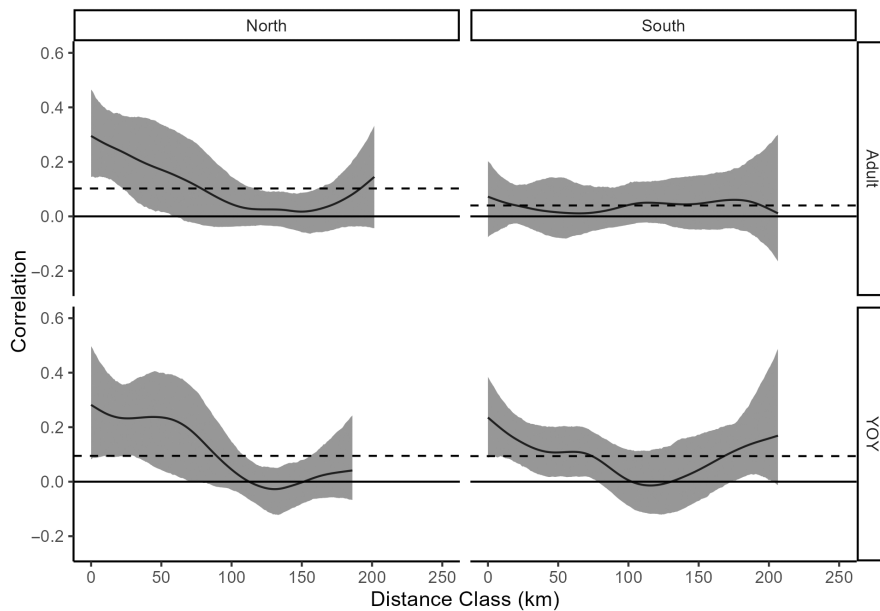
3.2 | Hierarchical model

Lacking random effects, predictive ability of the climate effect models was modest. Bayesian p-values for mean and coefficient of variation of pass 1 abundance were 0.35 and 0.61 (YOY) and 0.01
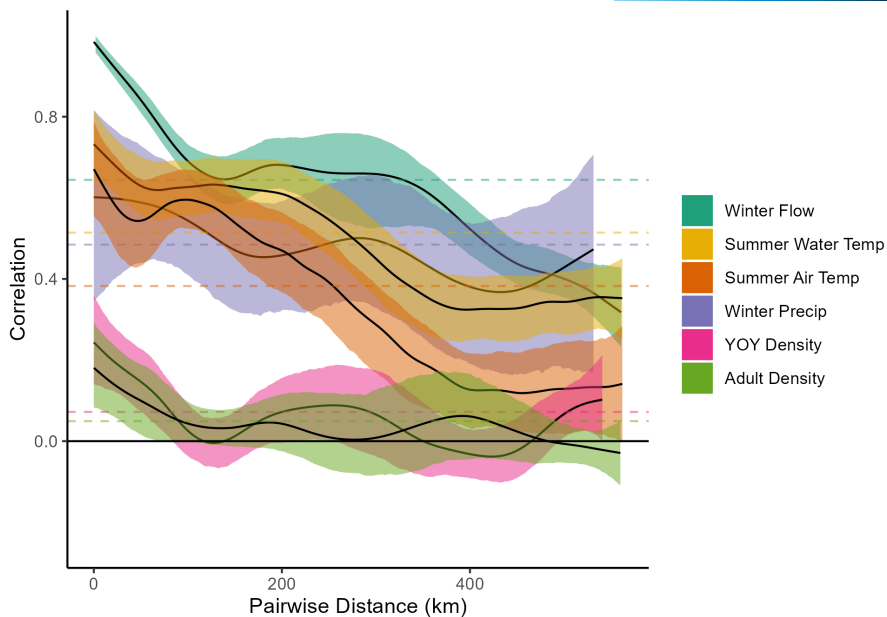
FIGURE 2 Spline correlogram of pairwise correlation in brook trout (*Salvelinus fontinalis*) log density (1995–2015) and selected climate variables for the southeast United States. Climate variables: mean estimated monthly winter (December–February) flow (1980–2015), mean daily observed summer (June–September) air temperature (2010–2015), mean daily observed summer water temperature (2010–2015), and total observed monthly winter precipitation (2008–2013). Shading indicates 95% confidence envelopes. Dashed lines represent average pairwise correlations. *Climate data sources*: US Geological Survey NHDPlus v2.1, US Forest Service, National Oceanic and Atmospheric Administration.

FIGURE 3 Spline correlogram of brook trout (*Salvelinus fontinalis*) log density by life stage and sub-region. Shaded regions represent 95% confidence envelope. Dashed lines represent average pairwise correlations.

and 0.37 (adult). Predictive ability of the random effects models improved considerably, with Bayesian *p*-values for mean and coefficient of variation of pass 1 abundance of 0.46 and 0.57 (YOY) and 0.27 and 0.83 (adult). Electrofishing capture probability per pass (*p*) was higher for adults than YOY. Estimates of capture probability varied by agency, with the mean probability ranging from 0.47 (95% HPDI = 0.41–0.53) to 0.63 (95% HPDI = 0.62–0.65) for YOY and from 0.62 (95% HPDI = 0.58–0.67) to 0.77 (95% HPDI = 0.76–0.78) for adults (Figure S4).

3.2.1 | Overall climate effects across stream segments

Climate effects on brook trout abundance varied by life stage, as represented by posterior distributions of the mean parameters for μ_β (Figure 4). As predicted, YOY were more affected by climate than were adults, thus unless noted otherwise we focus here on YOY responses. At the regional scale (Figure 4), all three environmental covariates had negative effects on YOY abundance, while summer
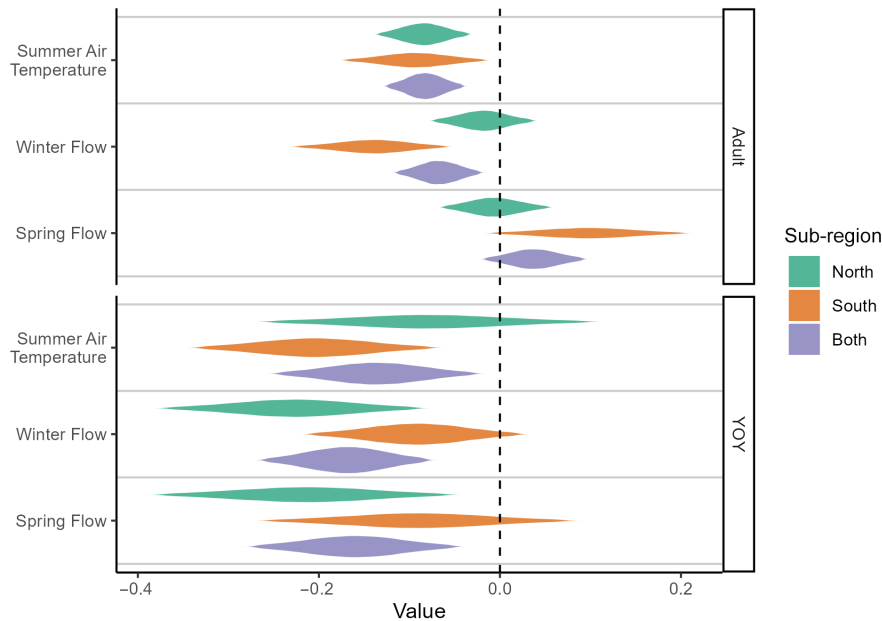
FIGURE 4 Ninety-five percent highest posterior density intervals (HDPIs) for climate effects on brook trout (*Salvelinus fontinalis*) log density by life stage and sub-region. Climate variables: average 0.9Q summer air temperature (year $t − 1$), max 0.9Q winter stream flow (year t), max 0.9Q spring stream flow (year t). *Data sources*: US Geological Survey NHDPlus v2.1, National Oceanic and Atmospheric Administration.

air temperature and winter flow had negative effects on adult abundance. Winter high flow had the strongest negative effect on YOY abundance (mean = −0.22; 95% HPDI = −0.3 to −0.15), closely followed by spring high flow (mean = −0.18; 95% HPDI = −0.27 to −0.09) and high temperatures in the previous summer (mean = −0.1; 95% HPDI = −0.2 to −0.01).

Covariate effects also varied by sub-region. As hypothesized, summer air temperature had a stronger effect on YOY in the south than in the north (mean = −0.22; 95% HPDI = −0.33 to −0.11 vs. mean = −0.03; 95% HPDI = −0.18 to 0.12). In the northern sub-region (symbolized in green in Figure 4), YOY abundance was predominantly driven by flow (winter flow mean = −0.25 and 95% HPDI = −0.36 to −0.14 and spring flow mean = −0.25 and 95% HPDI = −0.38 to −0.13), with no significant effect of summer air temperature (mean = −0.03; 95% HPDI = −0.18 to 0.12). In the southern sub-region (symbolized in orange in Figure 4), YOY abundance was primarily driven by summer air temperature (mean = −0.22; 95% HPDI = −0.33 to −0.11). A negative effect of summer air temperature on adult abundance (mean = −0.09; 95% HPDI = −0.13 to −0.05) was detected in both sub-regions. Overall, stream flows were the primary driver of YOY abundance over time in the northern sub-region, whereas summer air temperature was the most important driver of YOY abundance in the southern sub-region.

3.2.2 | Spatial heterogeneity in climate effects

Climate effects varied considerably among stream segments, a sign of local cross-scale interactions (Figure 5). The variance in local effects (σ_β^2) for winter stream flow on YOY abundance (mean = 0.21; 95% HPDI = 0.15–0.28) was smaller than that of spring stream flow (mean = 0.31; 95% HPDI = 0.23–0.4) or summer temperature

(mean = 0.37; 95% HPDI = 0.27–0.48; Figure 5). These results showed that winter stream flow had the most spatially homogeneous effect on YOY abundance. Variances in local climate effects on adult abundance were comparable, and 95% HPDIs overlapped (summer temperature variance: 0.06 [95% HPDI = 0.04–0.08], winter stream flow variance: 0.08 [95% HPDI = 0.06–0.1], spring stream flow variance: 0.09 [95% HPDI = 0.07–0.12]). Correlation analysis demonstrated that there was little influence of local habitat (e.g., land cover, elevation, channel slope, watershed area) on segment-specific responses to climate (β_i; Table S2). There was also little spatial structure in covariate effects on YOY brook trout abundance (segment-specific β_i, Figure S5).

3.2.3 | Synchrony

Estimates of segment-specific ICC values varied from 0.02 (95% HPDI = 0.001–0.05) to 0.84 (95% HPDI = 0.66–0.98) for YOY brook trout and from 0.0014 (95% HPDI = 0.00007–0.004) to 0.55 (95% HPDI = 0.09–1.0) for adult brook trout. YOY brook trout showed higher average ICC than adult brook trout (0.25 vs. 0.1), showing that YOY abundance is more synchronous across populations than adult abundance. On average, northern brook trout populations were more synchronous than southern populations (average YOY ICC: 0.53 vs. 0.26), which conforms with findings from the spline correlograms above. However, several of the most synchronous populations (highest YOY ICC) were in southern sub-region (Figure 6, but see Figure S7 for adult ICCs). There was only moderate correlation between ICC and local habitat variables (Table S3). There was considerable geographic heterogeneity in spatial synchrony (Figure 6), and segment-specific synchrony showed moderate spatial structure (Figure S6), showing that populations nearer to each other are more similar in temporal abundance patterns than populations

FIGURE 5 Local climate effects on brook trout (*Salvelinus fontinalis*) young-of-the-year abundance (model β_i). (a) Average 0.9Q summer air temperature (year $t-1$), (b) max 0.9Q winter stream flow (year t), and (c) max 0.9Q spring stream flow (year t). *Data sources*: US Geological Survey NHDPlus v2.1, National Oceanic and Atmospheric Administration.

(a) Summer Temp

(b) Winter Flow

(c) Spring Flow
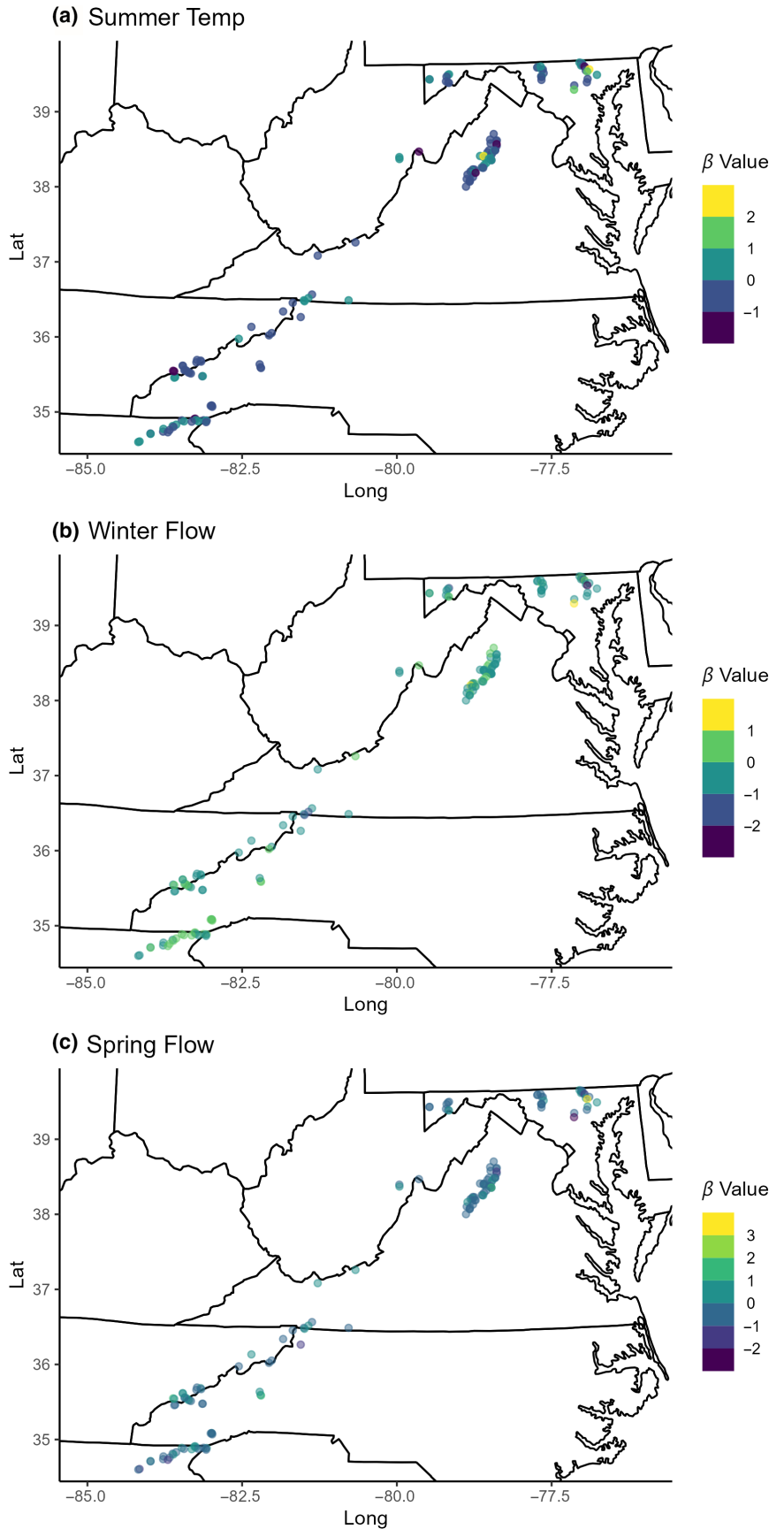
farther from each other. Variability in average abundance across all stream segments was lower than in individual segments (Figure S8), indicating a portfolio effect among the sampled populations. The coefficient of variation for interannual observed pass 1 abundance for YOY brook trout averaged across segments was 0.67, compared to a mean of 1.16 for individual segments.
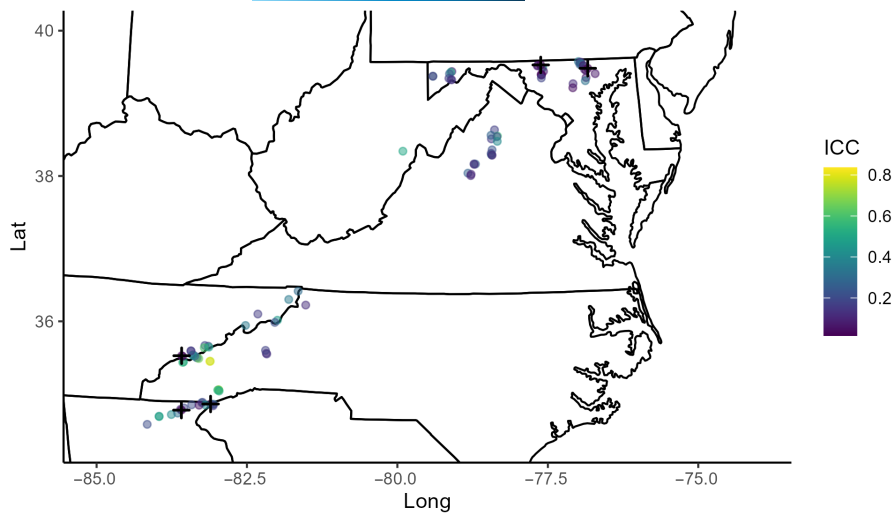
FIGURE 6 Intraclass correlation coefficient (ICC) values for young-of-the-year brook trout (*Salvelinus fontinalis*) abundance in the southeastern United States. High ICC values indicate synchrony relative to the temporal variation averaged across segments, while low ICC values indicate asynchrony. The five stream segments with lowest ICC (least synchronous) are indicated by "+".

4 | DISCUSSION

Our work synthesized count data from nine sources at 144 sites over 34 years, which represents one of the most thorough attempts to understand spatiotemporal variation of stream fish populations across a large geographic region (~1,000 km). Count data of this spatiotemporal coverage are few in freshwater fish populations (Comte et al., 2021). Our analysis not only reinforced previous findings that climate change would affect life stages differently via altered temperature and flow patterns (Kovach et al., 2016), but it also found that the magnitude of response heterogeneity of local populations to climate variation was higher than previously known based on analysis of individual, more geographically restricted datasets (Cattanéo et al., 2003; Kanno et al., 2016; Zorn & Nuhfer, 2007). Those populations that responded asynchronously to climate stressors may hold unique conservation value as this species faces a multitude of threats. Cross-scale interactions (Heffernan et al., 2014) were also observed between and within sub-regions, resulting in modest spatial autocorrelation and population synchrony relative to highly spatially autocorrelated abiotic variables. These findings indicate that climate change impacts on sensitive aquatic populations will be complex and that not all populations are equally vulnerable to these threats (Ebersole et al., 2020). Furthermore, they support the importance of population-level management for brook trout (Kazyak et al., 2022). Our work highlights an opportunity and the need for embracing spatially heterogeneous population responses in range-wide planning for brook trout and other species of conservation concern.

Spatial synchrony in trout populations was only modest when compared to highly synchronous temperature, precipitation, and stream flows, showing a first sign that the climate variables interacted with local conditions to generate spatially heterogeneous population responses. Previous studies of brook trout have reported stronger magnitude of spatial population synchrony than the current study, but they were much more limited in geographic extent (Kanno et al., 2016; Zorn & Nuhfer, 2007). Our new insight was gained only by synthetic analysis of multiple datasets at a broad spatial extent. Inferences on population synchrony depend inherently on geographic extent of investigations (Levin, 1992; Wiens, 1989), as further demonstrated by our parallel analyses of regional versus sub-regional data. Likewise, the identification of asynchronous outliers depends on the geographic extent and distribution of sampling sites. Still, our estimated spatial scales of trout synchrony are comparable to those of other freshwater species (Copeland & Meyer, 2011; Myers et al., 1997; Tedesco et al., 2004), and our average ICC values (i.e., magnitude of synchrony) were similar to those reported for other freshwater fish species (e.g., Michaletz & Siepker, 2013; Midway & Peoples, 2019) and considerably lower than those for terrestrial species (e.g., Canu et al., 2015; Grosbois et al., 2009; Lahoz-Monfort et al., 2011). Weaker synchrony of freshwater populations versus terrestrial populations may be due to stronger cross-scale interactions arising from fine-scale aquatic habitat heterogeneity (Benda et al., 2004; McCluney et al., 2014) and physical isolation of habitats by watershed boundaries (e.g., headwater streams) that prevent movement of aquatic organisms (Liebhold et al., 2004; Ranta et al., 1995). Additional research is warranted across taxa and ecosystems to elucidate relative strengths of these ecological mechanisms that determine magnitude and spatial scales of synchrony.

The most direct evidence of cross-scale interactions came from spatially heterogeneous climate effects on trout abundance. Our analysis showed that, when averaged across stream segments, YOY abundance was more sensitive than adult abundance to seasonal climate variation, a pattern commonly found in stream salmonids due mainly to vulnerability of the early life stage to substrate-mobilizing high flows and its diminished swimming abilities to cope with those disturbances (Kanno et al., 2016, 2017; Kovach et al., 2016). However, there was much variation among stream segments in the effect sizes (i.e., regression coefficients) of seasonal climate variables on trout abundance in this study. Importantly, the climate variables differed by spatial consistency in their effects on trout populations. Winter and spring stream flow both had similar negative effects on YOY abundance in both sub-regions, and winter stream flow had the most spatially homogeneous effect on YOY abundance when sub-regions were combined in the N-mixture model. Additionally,

the spline correlogram for YOY density exhibited the most similar shape to that of winter flow, with a defined dip at around 100 km Euclidean distance. It should be noted that as a modeled covariate, autocorrelation in stream flow at near distances was likely overestimated. Nonetheless, we reason that winter flow was the most important driver, among the three covariates tested, of the modest spatial autocorrelation and synchrony in YOY trout populations in this study. This inference is concerning regarding brook trout in the study area, which is projected to experience increased total precipitation during most of the year including winter (Alipour et al., 2020; Ingram et al., 2013; Pörtner et al., 2022). Wildlife managers could consider restoration that increases the natural resilience of stream systems to flooding such as improving riparian cover and in-channel habitat complexity (Giller, 2005).

With the exception of summer air temperature effects on adults, climate effects were spatially heterogeneous between sub-regions. We interpret these cross-scale interactions in the context of latitudinal gradients between the north and south sub-regions (Maitland & Latzka, 2022), where the southern sub-region was warmer in summer and the northern sub-region experienced higher magnitudes of winter and spring stream flows (Table 1). YOY abundance decreased following a hotter summer in the previous year in the southern but not in the northern sub-region. A potential mechanism for this decreased abundance is high adult mortality due to elevated summer temperature at more southern latitudes, which would lead to low spawner abundance in fall (Grossman et al., 2010; Sweka & Wagner, 2022). However, adult responses to summer air temperature did not differ between sub-regions in this study. Alternatively, this species delays or skips spawning in fall and gamete development may be reduced following a hot summer due to stress or reduced body condition (Pankhurst & King, 2010; Warren et al., 2012), and these sub-lethal effects could lead to lower YOY abundance in the following year. We speculate that regional differences in spring flow or even latitudinal temperature shifts (see Table 1) might explain why high spring flows resulted in lower YOY abundance mostly in the northern sub-region. Specifically, the magnitude of maximum spring flow was considerably higher in the northern sub-region, which would more likely result in stream bed scouring and YOY mortality in the northern versus southern sub-region. Plus, winter stream temperature during trout egg incubation was warmer in the southern sub-region relative to the northern sub-region (G. Valentine, unpublished data), which accelerates egg development in salmonids and generates latitudinal variation in hatch timing (Fitzgerald et al., 2021; Yamamoto et al., 1997). Consequently, body size of YOY in the northern populations may be smaller and more often subject to mortality-causing high flow events in spring than those in the southern populations, a hypothesis that needs to be tested with broad-scale studies of early life histories.

Population asynchrony and response heterogeneity in climate variation may also be due to biological diversity of brook trout populations distributed along the 1,000 linear kilometers of their range in this study. Stream organisms become locally adapted over evolutionary and ecological time scales (Fraser et al., 2011; Moody et al., 2015), which can generate spatially heterogeneous responses to environmental variation in species distribution ranges. For example, stream salmonid populations are differently adapted to thermal regimes based on their natal environment (Chen & Narum, 2021; Rogers et al., 2022), and life history traits such as age-at-maturation and longevity differ among populations (Neville et al., 2006; Rieman & Dunham, 2000). Biological and life history heterogeneity in salmonids can also produce a portfolio effect, where diverse responses lead to a stabilizing effect when considered in aggregate (Schindler et al., 2010, 2015). Brook trout populations in our study area are relegated to small headwater streams, where gene flow is limited among populations and populations are highly differentiated (Kazyak et al., 2022). Plausibly, the biological heterogeneity among brook trout populations, in addition to abiotic gradients in our study region, may be responsible for the degree of population asynchrony and response heterogeneity. A mechanistic understanding of how spatial heterogeneity in animal population responses is generated should offer an exciting avenue for additional research.

Although our analysis showed that climate effects on trout abundance differed among stream segments, our understanding is incomplete as to why the effects differed among them. Specifically, our exploratory analysis between segment-specific climate effects (β) and spatial covariates (e.g., elevation, watershed area, channel slope) did not establish strong linkages. This lack of correlation suggests that other factors may be responsible for the observed complex cross-scale interactions (Soranno et al., 2014). For example, groundwater discharge stabilizes temperatures over time and buffers aquatic habitat from warming (Brunke et al., 2003; Cartwright & Johnson, 2018). Groundwater influence can also provide suitable spawning and rearing habitat for fish (Blanchfield & Ridgway, 1997; Curry & Noakes, 1995). However, groundwater remains difficult to measure and predict over broad spatial scales such as that of our study (Kalbus et al., 2006). Likewise, locally patchy habitat characteristics such as riparian shading and in-stream wood availability can be readily missed when characterizing stream habitat at broad scales (Fernandes et al., 2011; Wohl et al., 2018). Localized extreme precipitation events are another factor with the potential to affect populations at small scales (Hickey & Salas, 1995). We recommend fine-scale, long-term studies in representative networks throughout the range to more fully understand climate effects on aquatic populations.

As predicted, the climate effects on trout populations were stronger for the YOY stage. Life stage-specific responses to flows are well documented in stream salmonids (Cattanéo et al., 2003; Kanno et al., 2017; Kovach et al., 2016). Early life stages of trout suffer high mortality when elevated flows mobilize stream bed substrates, as corroborated in this study by diminished YOY abundance following wet winter and spring in this fall-spawning species. Because YOY abundance in the current year is a good predictor of adult abundance in the following year (Kanno et al., 2016, 2017) and higher current adult abundance also typically leads to more YOY fish in the following year (Grossman et al., 2010; Sweka & Wagner, 2022), climate effects on trout abundance could persist for more than a single year.

That said, heterogeneous responses to climate variables between life stages may provide a demographic portfolio effect (Diamond et al., 2013; Dybala et al., 2013; Schindler et al., 2015) to buffer trout populations from climate change as long as unfavorable seasonal temperature and flow conditions do not occur frequently over consecutive years (Kanno et al., 2015).

Spatially heterogeneous and asynchronous population responses to climate have implications for the conservation of this and other threatened species at their range edges. Previous studies have assumed homogeneous and synchronous population responses to climate change in salmonids (Meisner, 1990; Rahel et al., 1996), and up to 97% habitat loss was projected for brook trout populations in the southern Appalachian Mountain streams (Flebbe et al., 2006), which corresponds to the southern sub-region of our current study. Although climate change is undeniably a major threat to the sensitive coldwater fish, our results demonstrate the importance of considering spatial heterogeneity and recognizing that some populations are more likely to persist than others in a changing climate. This finding underscores the importance of maintaining connectivity between populations, as demographic responses to environmental changes can vary within stream networks and connectivity increases the likelihood of demographic rescues (Tsuboi et al., 2022). A key challenge lies in identifying a set of priority conservation populations in a landscape in an increasingly uncertain and non-stationary environment (Heller & Zavaleta, 2009; Mejia et al., 2023). Our results inform this challenge by identifying highly asynchronous populations. Using gradients of population synchrony and heterogeneity to climate variation, priority conservation populations may be identified so that a portfolio of populations with a range of climate responses could be targeted for protection and restoration to buffer against climate change impacts (Raiho et al., 2022; Rosenberg et al., 2000). In this study and others, asynchrony among local populations contributed to this portfolio, diminishing temporal variation in region-scale abundance when local populations were aggregated (Hilborn et al., 2003; Schindler et al., 2010, 2015). This type of landscape-level planning is most effective when coupled with abiotic data to identify populations that are most likely to be resilient to climate change (i.e., climate refugia) (Ashcroft, 2010; Cartwright & Johnson, 2018; Larios-López et al., 2019; Mejia et al., 2023; Morelli et al., 2020). By investigating trends in population responses at multiple scales, our approach can inform conservation planning for an uncertain future. Finally, our methods are applicable to other wide-ranging aquatic species with spatially and temporally replicated datasets.

AUTHOR CONTRIBUTIONS

George P. Valentine: Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing – original draft; writing – review and editing. **Xinyi Lu:** Conceptualization; methodology; software; validation; writing – review and editing. **Evan S. Childress:** Conceptualization; resources; writing – review and editing. **C. Andrew Dolloff:** Resources; writing – review and editing. **Nathaniel P. Hitt:** Funding acquisition; resources; writing – review and editing. **Matthew A. Kulp:** Conceptualization; resources; writing – review and editing. **Benjamin H. Letcher:** Funding acquisition; resources; writing – review and editing. **Kasey C. Pregler:** Methodology; writing – review and editing. **Jacob M. Rash:** Conceptualization; funding acquisition; resources; writing – review and editing. **Mevin B. Hooten:** Conceptualization; funding acquisition; methodology; project administration; validation; writing – review and editing. **Yoichiro Kanno:** Conceptualization; funding acquisition; methodology; project administration; resources; software; supervision; writing – original draft; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are archived at sciencebase.gov in http://doi.org/10.5066/P9DQID6G.

CODE AVAILABILITY STATEMENT

Code can be found online at github.com/gpvalentine/SE_Trout.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.