**Introduction**

Water temperature is a key component of lotic ecosystems, determining species composition, organismal growth, and ecosystem functions and productivity (Caissie, 2006; Poff et al., 2002). Stream temperatures have risen in the last few decades (Kaushal et al., 2010) and will continue to rise as global climate change accelerates (Pörtner et al., 2022; van Vliet et al., 2013). Warming water temperature poses a major threat to the persistence of coldwater organisms, but warming rates are not spatially homogeneous due to surface-groundwater interactions and watershed and localized habitat characteristics (Lisi et al., 2013, 2015; Winfree, 2017). Identifying characteristics of stream habitats that offer refuge from climate warming and predicting their locations is critical to coldwater conservation planning (Ebersole et al., 2020).

However, a challenge lies in locating climate refugia for coldwater organisms over a broad geographic extent. Stream temperature is influenced by a multitude of atmospheric, hydraulic, and landscape characteristics and processes (Caissie, 2006; Lisi et al., 2015; Poole & Berman, 2001; Webb et al., 2008). Physical temperature models incorporate solar radiation, air-water heat transfer, evapotranspiration, and groundwater input (Caissie, 2006; Kelleher et al., 2012; Lalot et al., 2015; Sinokrot & Stefan, 1993). These processes may differ spatially due to local hydrology, riparian shading, and local landcover (Chang & Psaris, 2013; Dugdale et al., 2018; Garner et al., 2015; Mayer, 2012). These process-based modeling approaches are hard to replicate at many sites, especially for predicting temperatures at unsampled sites and consequently strategizing landscape and regional conservation efforts.

Alternatively, statistical approaches based on the relationships between stream and air temperatures have proliferated to characterize thermal variation among streams (Crisp & Howson, 1982; Erickson & Stefan, 2000; Mackey & Berrie, 1991; Mohseni et al., 1998; Mohseni et al., 1999; Morrill et al., 2005; Stefan & Preud’homme, 1993; Webb et al., 2008; Zhu et al., 2018). Stream-air temperature relationships have been represented by linear (REF) or nonlinear (i.e., logistic) regression (Mohseni et al., 1998; Mohseni & Stefan, 1999). The nonlinear approach is suited in regions characterized with low (<0 °C) and high (>25 °C) air temperatures. Specifically, stream temperature typically stays 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 hourly, daily, and weekly (Caissie et al., 2001; Stefan & Preud’homme, 1993; Webb & Nobilis, 1997), with a time lag between stream and air temperature diminishing over longer temporal scales and thus the tightest stream-air temperature relationships at weekly scales (Kelleher et al., 2012). Sensitivity of stream temperature relative to changes in air temperature is typically used as an indicator of groundwater input, where more temporally stable stream temperature amid air temperature fluctuations signifies climate refugia (Beaufort et al., 2020; Hare et al., 2023; Kelleher et al., 2012).

Despite our increasing knowledge of spatial variability in thermal sensitivity, uncertainty persists as to whether this spatial variability can be sufficiently explained and predicted by readily available watershed and hydrological data at the national and regional scale (e.g., National Hydrography Dataset (NHD) in the USA). These broad-scale data sets inherently provide coarse-scale habitat characterization; for example, the NHD contains habitat 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 climate refugia. Despite potential limitations, spatial variability in thermal sensitivity has been attributed to coarse-scale habitat metrics such as riparian conditions, stream size, and geology (Beaufort et al., 2020; Chang & Psaris, 2013; Mayer, 2012; Tague et al., 2007; Toffolon & Piccolroaz, 2015). As broad-scale stream habitat data become increasingly available, it is important to test their ability to explain and predict thermal sensitivity over a broad geographic extent to inform management of coldwater species of conservation concern.

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

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

**Discussion**

Our work represents one of the most geographically extensive analyses of thermal habitat for an aquatic species of conservation concern. The paired stream-air temperature data showed much thermal variation among 203 sites distributed along approximately 1,000 km, including some sites where stream temperatures were stable over time (weekly average < 15 °C) and others where stream temperatures warmed readily with increasing air temperatures. Spatial thermal variability has been observed in other brook trout studies conducted over more geographically confined areas (Kanno et al., 2014; Trumbo et al., 2014). Given the thermal heterogeneity over space and upper thermal limits of brook trout (22-24 °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 populations over a long period of time and serve as climate refugia. Notably, principal components derived from landscape variables in the NHD explained XX % of variation in thermal sensitivity among sites, showing that readily available regional landscape data may be sufficient for describing why thermal heterogeneity exits in a region. Overall, our study highlights the importance of embracing spatial thermal variability for identifying thermal refugia and using this knowledge in maximizing the chance of sustaining coldwater species in a large landscape.

We found a latitudinal pattern of thermal refugia locations, where thermally resistant sites were clustered in the southern area (i.e., North Carolina and Tennessee) of the study region. More thermally resistant sites were characterized with cooler maximum average weekly temperatures, and this correlation between different thermal metrics provided further support for the robustness of our thermal refugia predictions. We reason that the latitudinal pattern of thermal sensitivity was due to spatial gradients of altitude in this study area, where altitude peaks in the southern area and decreases northward. Altitude has frequently been linked to thermal regimes that differ over space (Isaak et al., 2017; Maheu et al., 2016; more REF). Our finding of more thermally resistant sites in the southern area corroborates with REF, who suggested that brook trout populations would more likely persist in that area than farther north due to projected thermal conditions, and contrasts with Flebbe et al. (2006), who did not account for spatially heterogenous stream-air temperature relationships and projected a nearly complete eradication of brook trout populations there in warming scenarios. Smaller clusters of climate refugia were also identified in the northern area such as eastern West Virginia and eastern Maryland. In general, thermal sensitivity of stream temperatures was spatially autocorrelated resulting in clusters of climate refugia, although this is not always the case in our data set and previous studies (Kanno et al., 2014; Snyder et al., 2015). Nevertheless, our work is useful for identifying general clusters where thermal refugia mostly likely occur, to guide where conservation and restoration might be prioritized.

In addition to the conspicuous latitudinal pattern of climate refugia locations, the principal components of landscape variables revealed complexities of thermal controls over space. In general, water temperature was more buffered against changes in air temperature when streams were located in XXXX. The degree of groundwater influence, represented by baseflow index, has consistently been identified as a determinant of thermal sensitivity (Beaufort et al., 2020; Briggs et al., 2018; Johnson et al., 2020; Kelleher et al., 2012; Tague et al., 2007). In our study, metrics of water velocity (second and four axes of PCA) explained spatial variation in thermal sensitivity better than groundwater. We surmise that water velocity might be surrogates of 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). Similarly, sediment, geology, and landcover may be linked to processes that affect stream temperature resiliency such as the water table depth and water retention in soils (Monk, 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 were needed in predicting thermal sensitivity for all stream segments potentially occupied by brook trout in the study area. Previous research often used a limited number of landscape covariates to characterize spatial thermal variability (Beaufort et al., 2020; Kelleher et al., 2012; Tague et al., 2007), and multivariate approaches should be considered more frequently especially for predictive purposes.

The spatial grain of our thermal sensitivity predictions was for NHD stream segments, given the landscape data availability for the large geographic extent of this study. However, thermal heterogeneity can occur within stream segments (Fullerton et al., 2018; Kalbus et al., 2016; Selker et al., 2006) and aquatic organisms may cue in highly localized areas of cold stream temperature to avoid unsuitably high temperatures in summer (Matthews & Berg, 1997; Sullivan et al., 2021). Additional research is warranted to investigate availability of spatially confined thermal refugia in stream segments that were predicted to respond sensitively to air temperatures, and this requires methods to characterize fine-scale thermal heterogeneity (e.g., fiber-optics cable; Selker et al., 2006) and habitat use by aquatic organisms (e.g., temperature tags; Hahlbeck et al., 2022). In the meantime, stream segments identified as thermal refugia in our study should be validated and this could be accomplished by deploying additional pairs of stream and air temperature loggers.

In conclusion, this study demonstrates that spatial thermal variability can be characterized by readily available landscape variables for a large region. This knowledge is critical for managing coldwater species in a warming climate and identifying locations of climate refugia (Jones et al., 2014). Importantly, climate refugia should be defined and located based on stream thermal regimes and 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.

**## Sentences below could be added to the Discussion, but it needs to be described and integrated better.**

Our estimates of slopes for weekly linear regressions are roughly in line with those reported in previous reports [see Table 3 in @beaufort2020]. Linear slopes were generally lower/higher than findings from other studies, indicating that water temperatures at trout habitat in the southeast US are more/less buffered than those in other regions.

We found that temperature values summarized at weekly intervals outperformed those summarized at daily intervals. This finding is in agreement with those of other researchers that have compared model fits at multiple temporal scales [@stefan1993; @kelleher2012; @morrill2005]. The supposed reason for this is that by aggregating across a broader temporal interval, the time lag between air and water temperatures can be negated [@stefan1993].

Our gap analysis revealed that a majority of thermally stable brook trout habitat in the study area already lies within protected areas. These protected areas are often highly conserved [@PADUS2022], and at the least are protected from the conversion of natural land cover to anthropogenic land cover. Conversely, this means that nearly half of this habitat remains vulnerable to human impacts and land use conversion. Brook trout are an aquatic indicator species, and they often cohabitate with other sensitive and threatened taxa [@vandusen2005; @vile2018]. Managers and conservationists seeking to conserve land in this region should incorporate stream thermal stability into their considerations.

A common drawback of studies of thermal stablity is that air temperatures are derived from model outputs or the most convenient meteorological station [@beaufort2020; @hare2021; @kelleher2012]. This means that trends in air temperatures used for analysis may not reflect the true trends influencing stream temperature at the local scale [@kanno2014]. Solar radiation and the influence of local topography have been shown to substantial influence variation in the microclimate across the landscape, particularly in mountainous areas [@aalto2017; @tscholl2022]. Furthermore, weather stations are commonly situated in open, flat areas where they miss the thermal effects of topography and tree cover [@defrenne2016; @graae2012]. We overcome this problem by using air temperatures measured in-situ at the same locations where water temperatures are measured. By using these paired air and water temperature loggers, our study design therefore allows the consideration of highly local atmospheric influence on stream temperature.