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Within-Reach Temperature Heterogeneity is Limited in a Southern Appalachian Stream Network: Implications for Climate Change Refugia and Reach-Scale Temperature Mapping

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PROJECT TITLE

Within-reach temperature heterogeneity is limited in a southern Appalachian stream network: implications for climate change refugia and reach-scale temperature mapping

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ABSTRACT

Water temperature is an important determinant of species distributions in flowing freshwater environments, however anthropogenic climate change threatens many freshwater species as suitable habitat shifts upslope or is expunged. These distribution changes will depend, in part, upon within-reach temperature heterogeneity and its potential to provide cold refugia. We monitored stream temperatures at 162 locations in six streams of the Little River watershed (Blount County, TN) during the summer of 2018 with the goal of assessing fine scale temperature heterogeneity (FSTH) and identifying local environmental factors driving within-reach temperature heterogeneity. Overall, we show that FSTH increases with mean air temperature and stream size, as well as from high to low elevation. Even so, FSTH was greater among reaches and seasons than it was within them, suggesting limited thermal refugia. These findings suggest that thermally sensitive biota will need to move to upslope reaches to seek thermal refuge as climate warming progresses. These findings also validate stream temperature modeling and mapping applications performed at the spatial resolution of confluence-to-confluence stream reaches based on GIS data layers.

Keywords: climate change, fish conservation, thermal refugia

INTRODUCTION

Water temperature is an important determinant of ecological processes and species distributions in freshwater ecosystems. It influences growth and metabolic rates of individuals, abundance and distribution of populations, and trophic interactions within communities (Boltaña et al. 2017, Cassie 2006, Winder 2004). Temperature regimes in flowing freshwaters vary along natural environmental gradients. For example, water temperature generally increases along the fluvial gradient (from small, high elevation streams to large, low elevation streams) and may also be impacted by gradients of groundwater input, snowmelt, or solar radiation (Caissie 2006, Fullerton et al. 2015). In addition to natural gradients, anthropogenic activities alter water temperatures in freshwater ecosystems in numerous ways. Water temperature is directly influenced by rising air temperatures resulting from climate change and indirectly influenced by landscape alterations, such as land use change, reduced riparian shading, or flow modification, which impact air/water temperature relationships (Woodward *et al.* 2010, Torgersen *et al.* 1999). Temperature alterations may negatively impact freshwater biodiversity by inducing habitat loss, range shifts, and novel species assemblages (Comte *et al.* 2013).

Recently documented trends and future projections indicate that populations of stream-dwelling organisms have and will continue to shift their distributions upslope and poleward to track suitable thermal habitat as a consequence of climate change. For example, Comte & Grenouillet (2013) found that most of the 32 species analyzed in French streams shifted their distributions upslope between the 1980s and 2000s. Similarly, Hickling et al. (2006) documented that 15 freshwater fish species and 14 aquatic insect taxa in Britain had shifted their distributions poleward and upslope during the middle and late 20th century. Forecasting studies project a continuation of warming impacts through the remainder of the 21st century. For example, Troia & Giam (2019) projected an increase in extreme heat events for streams in the southern Appalachian Mountains (southeastern USA) under 21st century climate change and a concomitant increase in the risk of physiological stress of four endemic fishes. Wenger et al. (2011) projected upslope shifts and distributional declines of native salmonid fishes in the Rocky Mountains (western USA) over the same time period. Whether these future projections come to fruition will depend, in part, on whether organisms have access to thermal refugia within their current geographic ranges (Hannah et al. 2014). For example, Isaak et al. (2017) demonstrated that high gradient stream reaches in the mountainous western United States will slow the upslope shift of isotherms, thus providing slow-climate-velocity refugia for thermally sensitive taxa. A shared assumption of these studies is that organisms responding to rising temperatures and seeking thermal refugia perceive thermal heterogeneity among, rather than within, stream reaches.

Another potential source of thermal refugia is fine-scale thermal heterogeneity (hereafter ‘FSTH’). FSTH refers to variations within broader water temperatures due to local factors such as riparian shading, groundwater inputs, flow, or thermal stratification (Arscott *et al.* 2001). This local environmental complexity increases habitat scale thermal variation, giving rise to ecologically important thermal refugia. Species can utilize microhabitats created by FSTH to exist at the extremes of their thermal tolerances (Cassie 2006). This is exemplified in a study examining behavioral thermoregulation of brook and rainbow trout in an Adirondack river. With summer water temperatures reaching the near lethal maximum for salmonids, the two trout species were able to use areas of thermal refuge near groundwater inputs to maintain average body temperatures cooler than ambient river temperatures (Baird & Krueger 2003). With warming climate trends on the rise, FSTH within waterways could be an important buffer for cool water species that would otherwise suffer habitat loss due to increased water temperatures. To mitigate species loss and better understand the impacts rising temperatures will have on species distribution and survival, it will be increasingly important to study these fine scale temperature occurrences.

Employing statistical models that identify environmental conditions driving water temperatures and that accurately predict water temperatures across stream networks is becoming increasingly important for conservation efforts. Such regional models typically predict water temperature at the spatial resolution of confluence-to-confluence stream reaches (hereafter 'reaches') because this is the scale at which GIS-derived landscape predictors are available (DeWeber & Wagner 2014, Isaak et al. 2017, Troia et al. 2019). For example, the National Hydrography Dataset (NHD) and the auxiliary StreamCat dataset facilitate the modeling and mapping of water temperature variation *among* the 2.65 million reaches in the contiguous United States (Hill et al. 2016, McKay et al. 2012). Nevertheless, these reach-resolution models do not account for FSTH maintained by riparian canopy gaps, groundwater input from the stream bed or bank, vertical thermal stratification in deep slow-flowing pools, and isolation of flow in off-channel habitats. High resolution modeling of regional temperature variations is much needed. More accurate models will decrease the disparity between modelled conditions and the true environmental conditions to which species are exposed. Fine scale temperature models will serve as better predictors for ecosystem management, which will be vital as temperatures rise over the next century.

In this study, we monitored stream temperatures at 162 locations in six streams of the Little River watershed (Blount County, TN) with the goal of assessing FSTH and the local environmental factors with which FSTH correlates. We established monitoring locations along gradients of landscape alteration, elevation, and stream size to identify both natural and anthropogenic drivers of FSTH. We sought to determine the extent and cause of FSTH occurrence within confluence to confluence points of stream reaches within the Little River watershed, as well as how FSTH varies between reaches. We also examined the relative influence of spatial and temporal variation on the stream temperatures. We predict that FSTH occurrence will increase with frequency as stream catchment size increases and elevation decreases because larger, slower streams at lower elevations typically are less mixed and, thus, more thermally heterogenous. We also predict that FSTH will be dependent upon other local environmental factors.

METHODS

Study Sites

We monitored water temperatures in six stream reaches within the Little River watershed (**Figure 1**). The Little River watershed is a tributary of the Tennessee River System, drains portions of the Blue Ridge Mountains and Ridge and Valley ecoregions, and hosts a rich variety of endemic fishes and other aquatic organisms (Stein 2002). Reaches were selected to represent gradients of elevation, land use and stream size (i.e., catchment area) (**Table 1**). Three reaches were established within the Great Smoky Mountain National Park, and drained high elevation forested portions of the Blue Ridge ecoregion. The other three reaches drained comparatively lower elevation portions of the Ridge and Valley ecoregion with higher agricultural land cover. Elevation, catchment area, reach length, and landscape characteristics were derived from the NHD and StreamCat datasets (Hill et al. 2016, McKay et al. 2012).

Field Methods

Within each of the six reaches, we established nine transects, each with three water temperature monitoring points (N = 27 monitoring points per reach). At each monitoring point, one Ibutton temperature loggers (Thermochron DS1922L) was deployed in a silicone caulk-sealed PVC housing to prevent exposure to moisture and secured in position by chaining the housing to a boulder or tree root. At each transect, a fourth logger was deployed on the north side of a tree trunk in open PVC housings to monitor air temperature All temperature loggers were programed to record temperature every 15 minutes.

Transects were spaced approximately uniformly along the length of each reach, but were positioned such that the diversity of mesohabitats (pool, riffle, run, side channel), riparian canopy gaps, and channel azimuths were proportionally represented. Within each transect, monitoring points were positioned in the mid channel and left and right margins (or side channel if present). To test for vertical thermal stratification in deep pools (sensu Nelson et al. 1994), buoyed logger systems were deployed at the three transects representing the deepest and slowest-flowing pools. At these transects, one logger was deployed at the bottom of the streambed, while another logger was secured to a foam buoy floating above the bottom logger. The top loggers attached to buoys were positioned approximately 5cm below the surface of the water. All other loggers recorded water temperatures at the bottom of streambeds.

We monitored temperatures at each of the six reaches during an early summer period (31 May to 14 July) and late summer period (24 July to 6 September). During each monitoring period, loggers were deployed for three consecutive days (**Table 1**). At each monitoring point, GPS coordinates were recorded, as was canopy cover (using a concave spherical densiometer), stream depth, logger vertical position (vertical distance from streambed), and lateral distance from bank.

Data Analysis

Data were analyzed in R using fBasics, car, lme4, ggplot2, chron, gridExtra, MuMIn, tidyr, pacman, packages. To ensure that only accurate temperature readings were used for data analysis, boxplots of outlier temperature data were made and reviewed in R. Resulting outliers were reviewed in the time series data from logger recordings. Flagged temperature recordings from before and after deployment and removal times were removed. Outliers that appeared to be due to recording errors were also removed. In most cases of data removal, it was due to point errors, where only one or two temperature recordings required removal from the time series. Occasionally, due to weather or circumstance, loggers were dislocated or exposed to air during the recording period. In such cases, all time series data recorded by the dislocated logger was removed.

Next, all temperature recordings from loggers in buoy pairs were isolated in the data for a separate analysis. Mixed effects models and paired boxplots were employed to compare temperatures from bottom and top loggers for each transect, site, and week. Upon finding that there was no significant difference in temperatures recorded at the top and bottom of buoy pairs, all top buoy temperature recordings were removed from the data set, leaving 24 logger time series recordings for each site. All temperatures in the following analyses are derived from loggers positioned at the bottom of streambeds.

After editing the temperature data, there were three full days of temperature recordings for each stream reach per monitoring period. A time series plot was used to show the temperatures of the 24 loggers within upstream and downstream reaches over the course of the three days, where temperature is logged every fifteen minutes. Linear regression plots were employed to visualize the standard deviation of the mean and mean maximum temperatures per stream reach for each of the three days in relation to elevation and stream size, as well as mean air temperatures for each monitoring period. Additionally, linear regression and mixed effects models were used to assess the effect on FSTH of environmental variables (canopy cover, lateral distance from bank).

RESULTS

Comparison of the temperature data by monitoring period revealed that mean temperature ranges were marginally smaller and mean stream temperatures were marginally warmer during the later monitoring period. Temperatures ranged approximately 1-2 degrees Celsius in upstream reaches and 2-3 degrees Celsius in downstream reaches during the early monitoring period and approximately 1-2 degrees Celsius in upstream and downstream reaches during the later monitoring period (**Table 2**). On average, stream temperatures were approximately 1 degree Celsius warmer during the later monitoring period (**Table 2**). Overall, downstream temperatures displayed greater variation between logger temperature recordings, while upstream temperatures were less variable. Even so, temperatures within the same reach tracked each other relatively closely, and there was greater FSTH between reaches than there was within reaches (**Figure 2**).

FSTH varied predictably with reach-level environmental variables. Specifically, FSTH of mean maximum stream temperatures was positively correlated with catchment area and mean air temperature and negatively correlated with elevation (**Figure 3**). There was no apparent correlation between FSTH of mean water temperatures and any of the reach-scale predictor variables (catchment area, mean air temperature, and elevation) (**Figure 3**). Therefore, subsequent analyses were performed using only mean maximum stream temperature metrics.

There was a significant temporal effect on mean maximum stream temperatures at the logger-scale, but, unlike at the reach scale, there was no significant spatial effect. Vertical position of buoyed loggers did not yield a significant difference between mean maximum temperatures (season 1: t = -1.6655, df = 17, p-value = 0.1141; season 2: t = -1.6434, df = 17, p-value = 0.1187). Summary statistics of mixed effects models revealed monitoring period had a significant effect on mean maximum stream temperatures; however, also revealed canopy cover and lateral distance from bank to have no significant impact (season: t= 17.0765738, lateral position: t= 0.2944239, canopy cover: t= -0.2865618) (**Figure 4**). This suggests there is a temporal effect on water temperature at the point resolution; however, because lateral position and canopy were not significant, there was not a spatial effect on temperature at the point resolution.

DISCUSSION

Freshwaters are among the most diverse ecosystems in the world and are disproportionately affected by climate change due to isolated habitat and species' limited dispersal ability (He *et al.* 2019, Woodward *et al.* 2010). Specifically, rising annual temperatures due to anthropogenic activity threaten many freshwater species as suitable habitats are shifted or expunged (Knouft & Ficklin 2017). In a study examining brook and rainbow trout populations in Southern Appalachian streams, a predicted 53%-97% of trout habitat is to be lost due to temperature increases (Flebbe *et al.* 2006). Similarly, a study encompassing 57 fish species in the U.S. predicted that thermal habitat for cool water fish species could be reduced by 36% due to climate change (Cassie 2006). Such predictions are of major conservation concern as freshwater biodiversity continues to decline at a faster rate than is observed in marine or terrestrial systems (Harrison *et al*. 2018).

These predictions are hinged on the assumption that within-reach temperatures are uniform, with little or no opportunity for thermal refugia between confluence-to-confluence segments of a stream reach. Our findings support such predictions drawn from reach level temperature modeling. Mean heterogeneity across reaches for maximum daily temperature (mean range across reaches = 1.22°C) and minimum daily temperature (mean range across reaches = 0.80°C) was below 2°C in the observed segments of the Little River watershed. Thus, the prediction error of reach-resolution models (i.e., 1-2°C) is consistent with the within reach variation observed in the present study. In environments of limited thermal refugia such as in this study, species may be forced to shift their distributions to track their thermal tolerances.

Though there was modest FSTH in lower elevation streams, heterogeneity observed in this study was predominantly explained by reach-scale environmental factors (i.e. elevation and stream size). Moreover, while there was a significant temporal effect on FSTH at the point resolution, there was no significant environmental effect. This suggests that fish must disperse to streams of different size and elevation rather than utilize microhabitats created by geomorphological units if they are to find refuge from thermal maxima. However, dispersal is dependent on upstream connectivity and individual dispersal ability of each species (Troia *et al.* 2019). Thus, conservation efforts in systems with limited thermal refugia should be focused on smaller-bodied species with limited dispersal abilities. Systems of reduced connectivity with numerous small-bodied fishes are therefore of special conservation concern. This bears special significance in Southern Appalachia, where small-bodied minnows and darters are the two most species rich groups found in the region (Troia *et al.* 2019).

Though our study supports the accuracy of reach resolution temperature models that are currently used in climate predictions, special conservation efforts should be made to protect stream habitats found to offer viable thermal refugia. Our study lends support for current climate predictions in water systems such as the Little River watershed; however, such predictions may not be as accurate in more thermally heterogenous systems witnessed in other studies (i.e. Baird & Krueger 2003; Ebersole, Liss, & Frissell 2001; Kaandorp V. *et al*. 2019; Kanno *et al.* 2014; Nielson *et al.*1994). For instance, brook and rainbow trout were able to use areas of thermal refuge to maintain average body temperatures cooler than that of an Adirondack river (Baird & Krueger 2003). Additionally, steelhead in Northern California streams were documented relying on thermally stratified pools to avoid main water temperatures at the high extreme of their tolerance (Nielson *et al.*1994). Often, these studies found groundwater input to play a major role in FSTH occurrence (Baird & Krueger 2003; Kaandorp V. *et al*. 2019; Kanno *et al.* 2014; and Mollenhauer *et al.* 2019). In systems with more groundwater contributions, finer scale modeling may be more appropriate.

In fact, the most thermally heterogeneous stream reach observed in this study, Ellejoy Creek, displayed thermal patterns that indicate groundwater contributions. Two loggers, each located on different transects, recorded consistently cooler daytime stream temperatures than those of the rest of the reach. These patterns were present in both the early and late summer seasons. Ellejoy creek also owes some of its thermal heterogeneity to another, unexplained pattern. Two loggers within the same transect recorded warmer daytime stream temperatures and cooler nighttime temperatures in both the early and late summer seasons. Despite this unique thermal pattern, environmental variables including canopy cover, lateral distance from bank, and logger depth were consistent with those of the rest of the reach. The loggers were in areas of high canopy cover (100%) and all were under 2 meters from the bank and between 30-60 cm in depth. This suggests that ground water and another environmental variable not captured within this study may impact within-reach temperature at the point scale.

Thus, it is possible that our study deviated from similar studies due to spatial and logistical limitations. Though loggers were placed at a fine resolution and in areas of habitat anomalies, much of the stream system could not be monitored. Consequently, it is possible to have missed recording key factors that influence FSTH such as areas of groundwater input. The duration and timing of monitoring periods in this study is another such noteworthy limitation. Temperatures at each of the 162 points were only monitored for three days per monitoring period (a total of six days at each of the 162 points) and none of the three days overlapped between sites (only one stream reach was monitored at a given time). This study would be improved with a longer monitoring duration and synchronized monitoring of all sites to better account for daily fluctuations in FSTH due to meteorological or flow conditions. For these reasons, our study may underestimate the thermal heterogeneity occurring within the Little River watershed.

In conclusion, freshwater fish populations must track thermally suitable habitat as isotherms continue to shift in the twenty-first century. Other studies have found that fishes accomplish this by means of dispersing up the fluvial gradient and engaging in behavioral thermoregulation by occupying microhabitats (Comte & Grenouillet 2013, Baird & Krueger 2003, Nielson *et al.*1994). Our findings indicate limited opportunity for the latter in our study system, because we observed minimal fine scale thermal heterogeneity within the Little River watershed during the monitoring period. Rather, further movements to reaches of different size and elevation appear to provide the only opportunity to access substantially (i.e., more than 1-2°C) warmer or colder temperatures. This dispersal will be dependent on upstream connectivity and individual dispersal ability of each species (Troia *et al.* 2019).

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REFERENCES

Arscott DB, Tockner K, Ward JV. 2001. Thermal heterogeneity along a braided floodplain river (Tagliamento River, northeastern Italy). *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 2359-2373.

Babaluk JA, Reist JD, Johnson JD, Johnson L. 2000. First records of sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) from Banks Island and other records of pacific salmon in Northwest Territories, Canada. *Arctic* **53**: 161-164.

Baird OE, Krueger CC. 2003. Behavioral thermoregulation of brook and rainbow trout: comparison of summer habitat use in an Adirondack River, New York. *Transactions of the American Fisheries Society* **132:** 1194-1206.

Boltaña S, Sanhueza N, Aguilar A, Gallardo-Escarate C, Arriagada G, Valdes, JA, … Quiñones RA. 2017. Influences of thermal environment on fish growth. *Ecology and Evolution*, **7**(17): 6814-6825.

Caissie D. 2006. The thermal regime of rivers: a review. *Freshwater Biology* **51**(8): 1389-1406.

Comte L, Buisson L, Daufresne M, Grenouillet G. 2013. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. *Freshwater Biology* **58**: 625-639.

Comte L, Grenouillet G. 2013. Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography* **36**: 1236-1246.

DeWeber, J. T., & Wagner, T. (2014). A regional neural network ensemble for predicting mean daily river water temperature. Journal of Hydrology, 517, 187-200.

Ebersole JL, Liss WJ, Frissell CA. 2001. Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. *Ecology of Freshwater Fish* **10**: 1-10.

Flebbe PA, Roghair LD, Bruggink JL. 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. *Transactions of the American Fisheries Society* **135**: 1371-1382.

Fullerton, A. H., Torgersen, C. E., Lawler, J. J., Faux, R. N., Steel, E. A., Beechie, T. J., ... & Leibowitz, S. G. (2015). Rethinking the longitudinal stream temperature paradigm: region-wide comparison of thermal infrared imagery reveals unexpected complexity of river temperatures. Hydrological Processes, 29(22), 4719-4737.

Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. Trends in ecology & evolution, 29(7), 390-397.

Hari RE, Livingstone DM, Siber R, Burkhardt-Holm P, Güttinger H. 2006. Consequences of climatic change for water temperature and brown trout populations in alpine rivers and streams. *Global Change Biology* **12**: 10-26.

Harrison I, Abell R, Darwall W, Thieme ML, Tickner D, Timboe I. 2018. The freshwater biodiversity crisis. *Science* **362**(6421): 1369

Hauer FR, Lamberti GA. (Eds.) 2011. Methods in stream ecology. *Academic Press*.

He F, Zarfl C, Bremerich V, David JNW, Hogan Z, Kalinkat G,… Jähnig SC. 2019. The global decline of freshwater megafauna. *Global Change Biology* **25**: 3883– 3892.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**: 450-455.

Hill RA, Weber MH, Leibowitz SG, Olsen AR, Thornbrugh DJ. 2016. The Stream-Catchment (StreamCat) dataset: a database of watershed metrics for the Conterminous United States. *Journal of American Water Resources Association* **52**: 120–128.

Isaak DJ, Young MK, Luce CH, Hostetler SW, Wenger SJ, Peterson EE,…Nagel DE. 2016. Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences USA* **113**: 4374–4379.

Isaak, D. J., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Nagel, D. E., Luce, C. H., ... & Chandler, G. L. (2017). The NorWeST summer stream temperature model and scenarios for the western US: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. Water Resources Research, 53(11), 9181-9205.

Kaandorp VP, Doornenbal PJ, Kooi H, Broers HP, de Louw PGB. 2019. Temperature buffering by groundwater in ecologically valuable lowland streams under current and future climate conditions. *Journal of Hydrology X* **3**: 2589-9155.

Kanno Y, Vokoun JC, Letcher BH. 2014. Paired stream–air temperature measurements reveal fine-scale thermal heterogeneity within headwater brook trout stream networks. *River Research and Applications* **30**(6): 745-7

Knouft JH, Ficklin DL. 2017. The Potential Impacts of Climate Change on Biodiversity in Flowing Freshwater Systems. *Annual Review of Ecology, Evolution, and Systematics* **48**: 111-133.

McKay L, Bondelid T, Dewald T, Johnston J, Moore R, Rea A 2012. *NHDPlus Version 2: User Guide*.

Mollenhauer R, Zhou Y, Brewer S. 2019. Multiscale Habitat Factors Explain Variability in Stream Fish Occurrence in the Ozark Highlands Ecoregion, USA. *Copeia* **107**(2): 219-231.

Nielsen JL, Lisle TE, Ozaki V. 1994. Thermally stratified pools and their use by steelhead in northern California streams. *Transactions of the American Fisheries Society* **123**: 613-626.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Stein BA, 2002. States of the Union: Ranking America's Biodiversity. Arlington, Virginia: *NatureServe*.

Torgersen CE, Price DM, Li HW, McIntosh BA. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. *Ecological Applications* **9**: 301-319.

Troia, M. J., & Giam, X. (2019). Extreme heat events and the vulnerability of endemic montane fishes to climate change. Ecography, 42(11), 1913-1925.

Troia, M. J., Kaz, A. L., Niemeyer, J. C., & Giam, X. (2019). Species traits and reduced habitat suitability limit efficacy of climate change refugia in streams. Nature ecology & evolution, 3(9), 1321-1330.

U.S. Geological Survey. 2019. National Hydrography Dataset, accessed October 2, 2018 at URL https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products

Vaughn CC, 2010. Biodiversity Losses and Ecosystem Function in Freshwaters: Emerging Conclusions and Research Directions. *BioScience* **60**(1): 25-35.

Winder M, Schindler DE. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* **85:** 2100–2106.

Woodward G, Perkins DM, Brown LE. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**(1549): 2093-2106.

TABLES

Table 1: Site information (elevation, catchment area, reach length, and percent forest) for each of the six stream reaches.

	MP	WP	EP	El	Na	LR
Reach characteristics						
In GSMNP	Yes	Yes	Yes	No	No	No
Length (m)	1,687	2,300	3,850	923	1,315	3,310
Percent Forest	99.62	99.41	99.43	56.29	41.65	79.74
Latitude *	35.6076	35.6568	35.6684	35.7739	35.8133	35.8000
Longitude *	-83.6375	-83.7102	-83.6997	-83.8233	-83.8835	-83.8874
Elevation (masl) *	787	353	352	268	254	254
Catchment area (km^2) *	17	47	154	94	46	705
Monitoring period						
Early summer						
Day 1	12-Jun	31-May	6-Jul	5-Jun	19-Jun	12-Jul
Day 2	13-Jun	1-Jun	7-Jul	6-Jun	20-Jun	13-Jul
Day 3	14-Jun	2-Jun	8-Jul	7-Jun	21-Jun	14-Jul
Late summer						
Day 1	21-Aug	5-Aug	4-Sep	24-Jul	15-Aug	29-Aug
Day 2	22-Aug	6-Aug	5-Sep	25-Jul	16-Aug	30-Aug
Day 3	23-Aug	7-Aug	6-Sep	26-Jul	17-Aug	31-Aug

* At downstream end of reach.

Table 2: Displays minimum, mean, and maximum water and air temperatures for all six stream reaches during each monitoring period.

	Early summer			Late summer		
	Min.	Mean	Max.	Min.	Mean	Max.
Water temperature						
MP	14.3	15.1	16.1	15.0	16.9	17.9
WP	16.1	17.4	18.8	17.5	18.9	20.5
EP	17.9	19.3	21.8	20.0	21.7	23.1
El	16.7	20.0	22.8	20.5	22.1	24.5
Na	20.2	21.5	23.5	19.2	20.9	23.8
LR	23.2	25.1	26.9	22.3	24.1	27.0
Air temperature						
MP	15.9	17.9	24.1	12.7	18.4	21.4
WP	16.8	20.2	28.2	17.6	22.0	29.3
EP	18.5	21.3	29.8	18.1	21.8	27.3
El	12.2	19.4	29.4	16.1	21.8	31.0
Na	20.0	23.4	33.9	17.8	23.4	34.7
LR	20.5	25.4	34.7	19.3	23.5	33.7

FIGURES

Figure 1. Locations of six water temperature monitoring reaches in the Little River watershed and nine transects within each reach. The green lined denotes the upper portion of the watershed located within Great Smoky Mountains National Park. Reach abbreviations are: Middle Prong Little River (MP), West Prong Little River (WP), East Prong Little River (EP), Ellejoy Creek (El), Nails Creek (Na), and Little River proper (LR).

Figure 2. Time series showing water temperature and air temperature among monitoring points from six reaches (different rows) during early summer (left column) and late summer (right column) monitoring periods. Each colored line is a different water temperature logger ($N = 27$ per reach) and each black line is different air temperature logger ($N = 9$ per reach). Reach abbreviations are: Middle Prong Little River (MP), West Prong Little River (WP), East Prong Little River (EP), Ellejoy Creek (El), Nails Creek (Na), and Little River proper (LR).

Figure 3. Standard deviation (SD) of mean and mean maximum stream temperatures plotted against reach-scale environmental factors: reach elevation, reach catchment size, and mean reach air temperature. SD of mean maximum temperatures is positively correlated with stream size and mean air temperature for summer seasons 1 &2, and negatively correlated with elevation. SD of mean temperatures was not correlated with any of the reach-scale environmental factors.

Figure 4. Plotted regression estimates of a linear mixed effects model testing the impact of temporal (season) and spatial (lateral position and canopy cover) factors on mean maximum stream temperatures at the logger-scale. There was a significant temporal effect, but no significant spatial effect on temperature.

Figure 1.

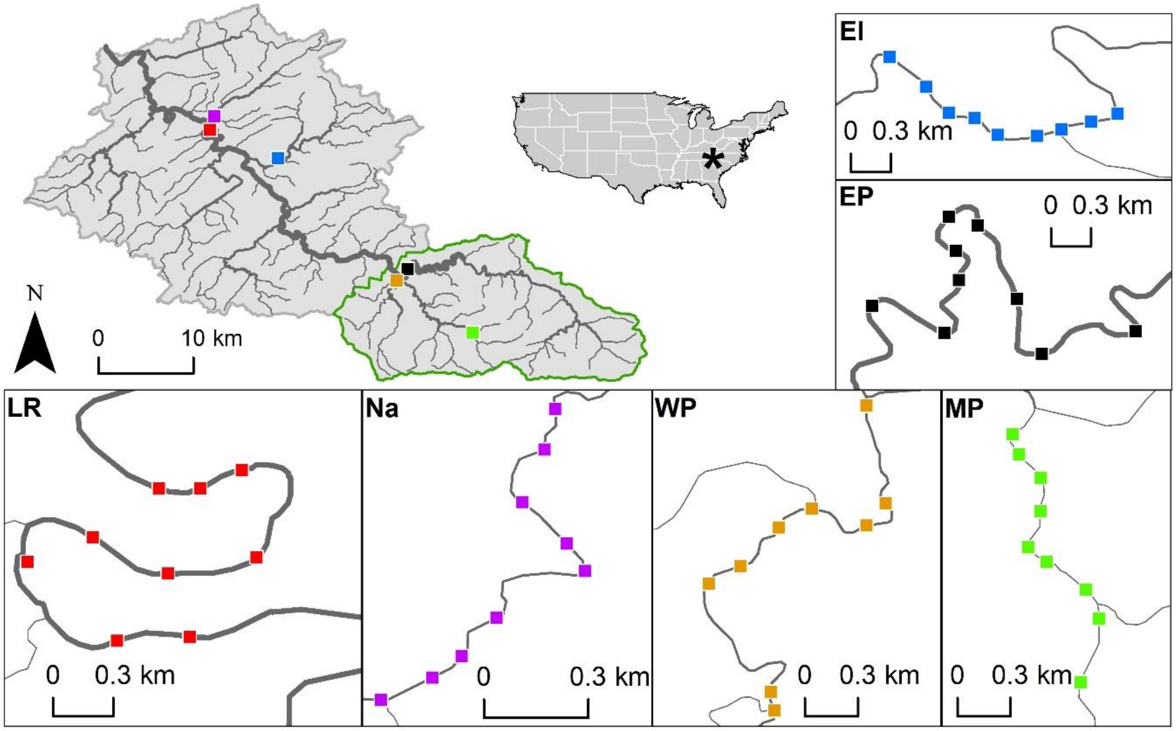


Figure 2.

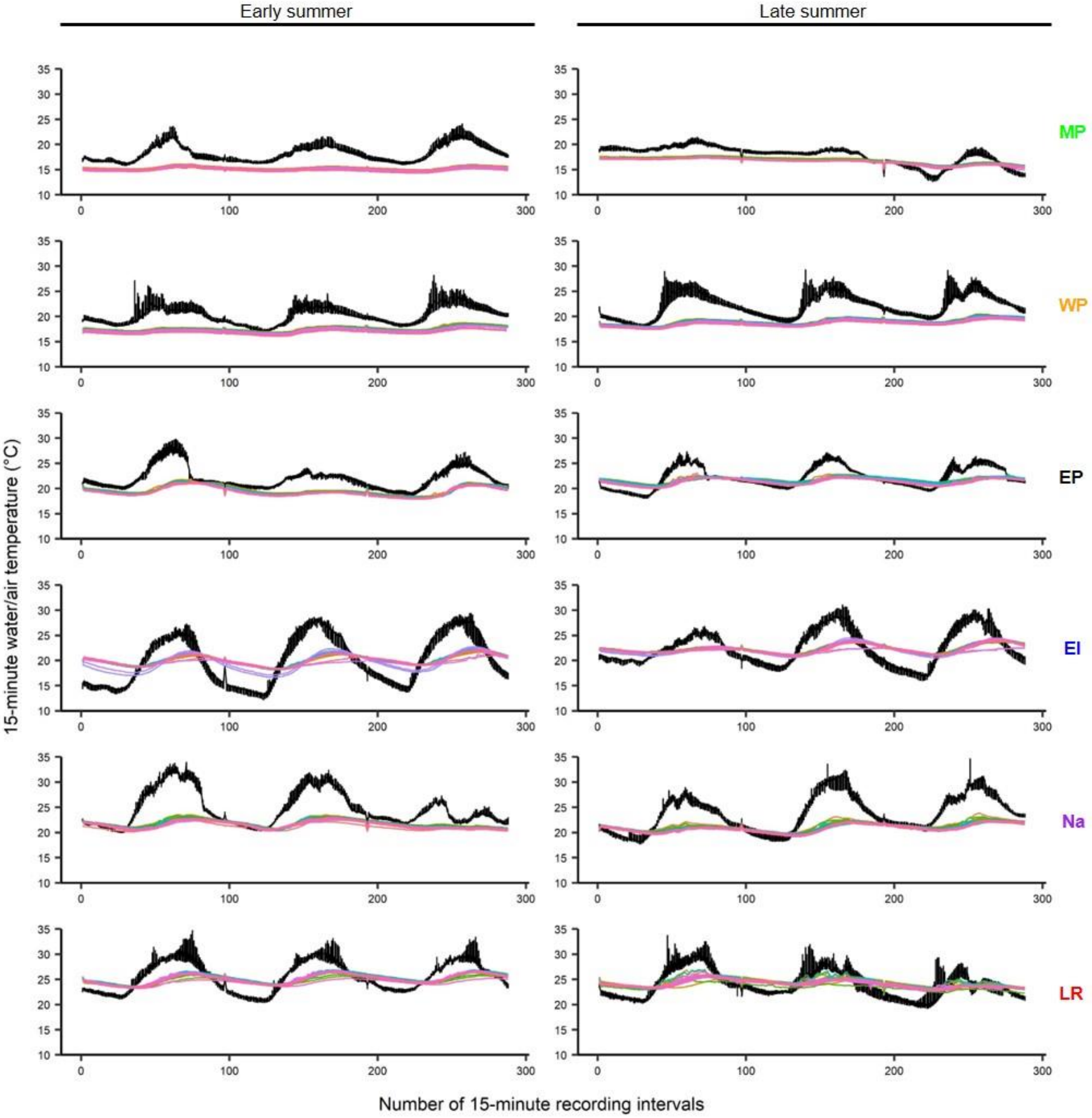
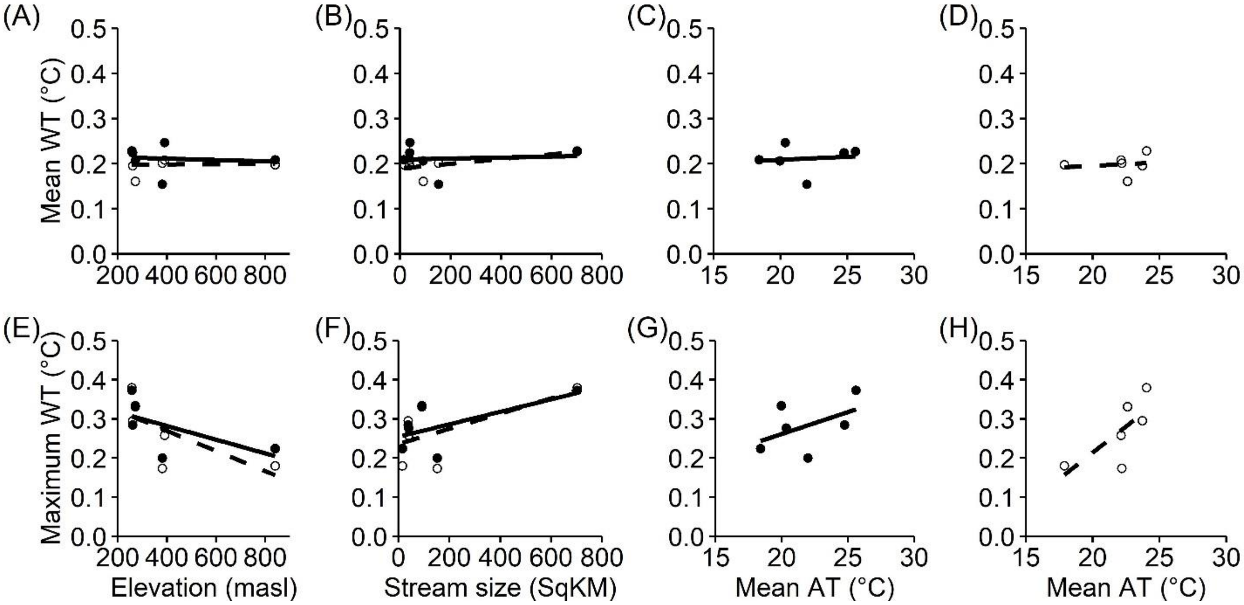

Early summer
Late summer
MP
WP
EP
EI
Na
LR
15-minute water/air temperature (°C)
Number of 15-minute recording intervals
35
30
25
20
15
10
0
100
200
300

Figure 3.



(A)
(B)
(C)
(D)
(E)
(F)
(G)
(H)
Mean WT (°C)
Maximum WT (°C)
0.0
0.1
0.2
0.3
0.4
0.5
200
400
600
800
0
15
20
25
30
Elevation (masl)
Stream size (SqKM)
Mean AT (°C)
Mean AT (°C)

Figure 4.