

Potential Effects of Climate Change on Appalachian Stoneflies (*Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata*)

Open-File Report 2021–1104–B

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By Marta P. Lyons, Catherine A. Nikiel, Olivia E. LeDee, and Ryan Boyles

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Conversion Factors

International System of Units to U.S. customary units

Multiply	Ву	To obtain					
Length							
millimeter (mm)	0.03937	inch (in.)					
meter (m)	3.281	foot (ft)					
kilometer (km)	0.6214	mile (mi)					

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows: $^{\circ}F = (1.8 \times ^{\circ}C) + 32$.

Abbreviations

EPA U.S. Environmental Protection Agency

JJA June through August

MACAv2 Multivariate Adaptative Constructed Analogs version 2

PET potential evapotranspiration

RCP4.5 representative concentration pathway 4.5 RCP8.5 representative concentration pathway 8.5

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By Marta P. Lyons,¹ Catherine A. Nikiel,² Olivia E. LeDee,¹ and Ryan Boyles¹

Abstract

Plecoptera (stoneflies) are an order of insects where most species rely on clean, fast-moving freshwater for an aquatic larval stage followed by a short terrestrial adult stage. Most species of Plecoptera seem to be restricted to specific stream types and thermal regimes. Climate-driven changes are likely to alter stream temperatures and flow, resulting in physiological stress, reduced reproductive success, and possibly latitudinal or elevational distribution shifts. This report focuses on climate projections and the resulting ecological effect for three species of Appalachian stoneflies: Remenus kirchneri, Acroneuria kosztarabi, and Tallaperla lobata. Although species-specific information is sparse for these three species, climate studies for other Plecoptera spp. are applicable. In the focal region, temperature is increasing and likely leading to increased stream temperatures. In response, Plecoptera spp. will likely experience physiological stress from increasing metabolic rates and energy demands concurrent with changing food quality and access. Warming temperatures and decreased larval energy stores are likely to contribute to lower adult body size and longevity, thus decreasing reproductive success. Whereas projected changes to precipitation and runoff are less certain, under drier future climate projections, decreased streamflow may further stress larval Plecoptera. Remenus kirchneri, A. kosztarabi, and T. lobata will likely retain stable permanent stream habitats for the analyzed future (2006–99). Changing climate is of particular concern for mountaintop species R. kirchneri and T. lobata because they may be unable to track shifts in suitable climate and habitat.

Purpose and Scope

The purpose of this report is to provide an overview of the direct and indirect effects of climate change on Plecoptera life cycle and habitat based on peer reviewed literature, government reports, and analysis of publicly available climate data. This report focuses on three order Plecoptera (stoneflies) species: Remenus kirchneri (Kondratieff and Nelson, 1995), Acroneuria kosztarabi (Kondratieff and Kirchner, 1993), and Tallaperla lobata (Stark, 1983). The focus region covers an area of the southeastern United States including parts of Tennessee, North Carolina, Kentucky, West Virginia, Ohio, and Virginia and contains the southern and central Appalachian Mountains (35–39.5° N, 85–77° W; fig. 1A). This spatial extent was chosen to capture the three species' current presence data. A more focused data analysis is provided for the study area outlined in figure 1A that consists of eight Watershed Boundary Dataset 8-digit Hydrologic Units (06010101, 06010103, 06010108, 05050001, 03040101, 03010103, 03010101, 02080203) (NRCS, 2022). This study area is spatially contiguous and contains the presence locations for the two narrowly distributed species (R. kirchneri and T. lobata) without spanning a large latitude/longitude range where spatial climatology differences may obscure signals of future change. Hydrologic units are also appropriate for delineating the study area because T. lobata, R. kirchneri, and A. kosztarabi have an aquatic habitat and will be sensitive to future changes in regional water balance. Ecological and climatological factors for these species are closely associated with the complex topography of the region, which is depicted in figure 1B. Full elevation distributions for the species presence records are shown in figure 1C, and a map of three elevation bands (below 450 meters [m], 450 to below 900 m, and 900 m and above) is shown in figure 1D.

¹U.S. Geological Survey.

²Oak Ridge Institute for Science and Education Research Participation Program.

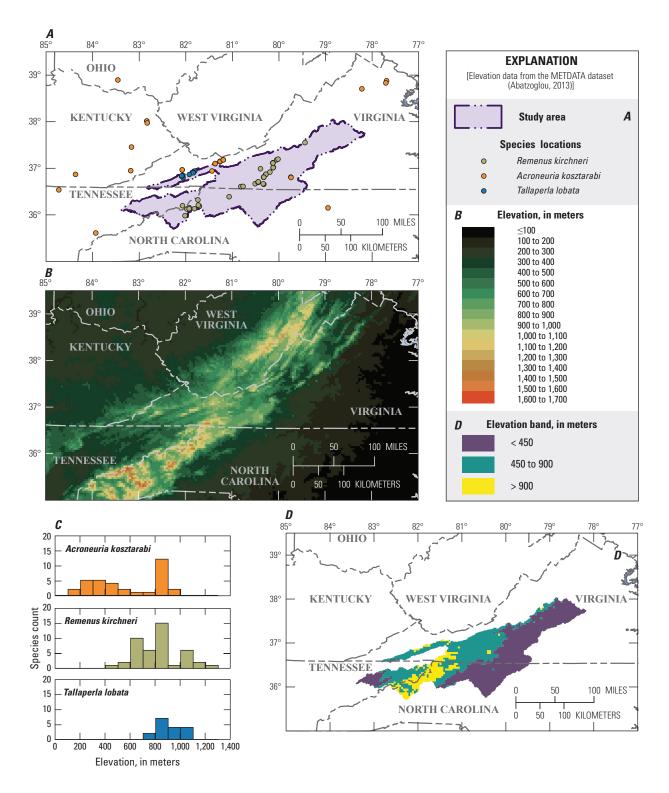


Figure 1. Study area, species locations, elevation, and elevation bands in Ohio, Kentucky, West Virginia, Virginia, Tennessee, and North Carolina. *A*, the study domain, species presence locations, and the main study area; *B*, elevation for the same area; *C*, distribution of METDATA grid cell elevation corresponding to recorded species locations; and, *D*, division of grid cells into three elevation bands. [Species locations from Verdone and Kondratieff (2018) and Verdone and others (2022)]

Data and Methods

To explore the potential range of future climate changes, we used downscaled projections for this region based on the Intergovernmental Panel on Climate Change Coupled Model Intercomparison Project Phase 5 models for two emissions scenarios: a moderate emissions scenario (representative concentration pathway [RCP] 4.5) and a high emissions scenario (RCP 8.5). The output from 20 global climate models with the necessary variables is statistically downscaled using the Multivariate Adaptative Constructed Analogs version 2 (MACAv2) method; this is a multistep constructed analog approach that establishes relations between global climate model output and historical climate observations. Outputs are bias corrected by climate variable to develop higher resolution and localized projections with about a 4-kilometer spatial resolution. The first realization (r1i1p1) of each model is used except for CCSM4 where the sixth realization (r6ilp1) is used. Output can be accessed through https://climate.northwestknow ledge.net/MACA/data portal.php (Abatzoglou and Brown, 2012), and the full list of models used can be found in table 1. MACAv2 was chosen because it is widely vetted, provides adequate spatial resolution to distinguish differences across the elevation gradients present in the Appalachians, and has been demonstrated to better capture signals in rainfall extremes and frequency as compared to other downscaled products (Wang and others, 2020; Wootten and others, 2021).

The observational dataset used here is the METDATA/ gridMET dataset, which is available daily from 1979 to 2022 at equivalent resolution to the MACAv2 data. The METDATA/gridMET dataset can be accessed through https://www.northwestknowledge.net/metdata/data/ (Abatzoglou, 2013). This dataset was developed using PRISM and NLDAS-2 gridded data (Mitchell and others, 2004; Daly and others, 2008). Elevation data from METDATA were used to determine the elevation of recorded species presence locations (fig. 1*C*) and to divide the study area into elevation bands (fig. 1*D*). This elevation dataset is used in the downscaling and bias correction of the climate data output, where elevation lapse rate plays a key role in correctly representing climate gradients over complex terrain.

Runoff projections are simulated using the Monthly Water Balance Model with the meteorological forcing from the MACAv2–METDATA described previously (Hostetler and Alder, 2016; Alder and Hostetler, 2021). Runoff is used in this report as a proxy for streamflow. Runoff data are available at the same spatial resolution as the MACAv2–METDATA climate data, and hydrologic projections are developed with this same set of climate models. This data correspondence allows for direct comparison of the meteorological and hydrologic variables at the same spatial resolution and during the same time periods for the same emission scenarios and set of models. Data are presented as model grid output, with no aggregation or routing. Runoff and streamflow are not directly analogous but are linked closely enough to be compared for validation of the hydrologic model output (Hostetler

and Alder, 2016). Model runoff is a sum of direct runoff partitioned from precipitation and supplemental runoff when soil storage is full. Although the spread of model projections used here better represent the range of plausible futures, the projections suffer from some of the necessary assumptions of a simple water balance model: (1) the model assumes a constant partitioning of 5 percent of rainfall to direct runoff, (2) the model does not account for variations in land use and vegetation, (3) the model does not simulate changes in long-term water storage, and (4) the model runoff calculation is dependent on a formulation of potential evapotranspiration (PET) from which it derives actual evapotranspiration (Hostetler and Alder, 2016).

An analysis of changes in precipitation minus PET is not used in this study. Although it is widely used in ecological studies that include a climate component, ultimately this metric is a proxy for water availability (Rangwala and others, 2021). Although a calculation of PET still affects the ultimate water balance and therefore measures of runoff, using the direct variable that has been validated against real world measures of streamflow rather than a proxy is preferable. Studies have determined that the choice of PET formulation affects future projections of drought metrics (Hoerling and others, 2012; Sheffield and others, 2012; Dewes and others, 2017; Feng and others, 2017; Milly and Dunne, 2017; Um and others, 2020). This limits the utility of any analysis involving PET.

Climate data are presented for four time period averages—a historical period (1971–2000) and three future time periods (2010-39, 2040-69, and 2070-99). These 30-year periods provide a long enough climate window to perform a robust analysis of period means and changes. At each time period, projections are provided for the two emissions scenarios: RCP4.5 and RCP8.5. Neither of these scenarios is presented as more likely than the other, and both are considered plausible. All 20 downscaled models were considered plausible future scenarios, but 5 models are presented for each future time period and emissions scenario to illustrate the spread of future climate conditions. These chosen models present a spatially consistent projection from an individual model rather than presenting an amalgamated median and range calculated at the individual grid cells. This presentation highlights how the magnitude and the spatial pattern of changes differ among model projections. Models are ranked based on changes for a given variable averaged over the study area (fig. 1A) and the minimum, 25th percentile, median, 75th percentile, and maximum change models are presented as a paneled figure with the same scale; thus, for example, the driest or warmest model in the early future period (2010–39) may not be the same as the driest or warmest model in the late future period (2070–99) and reflects the different rates of change among models and throughout the full future period. For clarity, the model used in each panel is marked by a letter in the bottom-right hand corner that refers to the corresponding model detailed in table 1.

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 Table 1.
 List of 20 downscaled global climate models from MACAv2-METDATA used in this study (Abatzoglou and Brown, 2012).

Letter ¹	Model	Group	Citation
A	BNU-ESM	College of Global Change and Earth System Science, Beijing Normal University (GCESS)	Ji and others (2014)
В	CCSM4	National Center for Atmospheric Research (NCAR)	Gent and others (2011)
С	CNRM-CM5	Centre National de Recherches Meteorologiques / Centre European de Recherche et Formation Avances en Calcul Scientifique (CNRM–CERFACS)	Voldoire and others (2013)
D	CSIRO-Mk3-6-0	Commonwealth Scientific and Industrial Research Organisation in collaboration with the Queensland Climate Change Centre of Excellence (CSIRO–QCCCE)	Rotstayn and others (2010)
Е	CanESM2	Canadian Centre for Climate Modeling and Analysis (CCCma)	Arora and others (2011)
=	GFDL-ESM2G	Geophysical Fluid Dynamics Laboratory (NOAA-GFDL)	Dunne and others (2012)
Ĵ	GFDL-ESM2M	Geophysical Fluid Dynamics Laboratory (NOAA-GFDL)	Dunne and others (2012)
Н	HadGEM2-CC365	Met Office Hadley Centre (MOHC)	Collins and others (2011)
I	HadGEM2–ES365	Met Office Hadley Centre (additional HadGEM2–ES realizations contributed by Instituto Nacional de Pesquisas Espaciais) (MOHC)	Collins and others (2011)
J	IPSL-CM5A-LR	Institut Pierre-Simon Laplace (IPSL)	Marti and others (2010)
K	IPSL-CM5A-MR	Institut Pierre-Simon Laplace (IPSL)	Marti and others (2010)
L	IPSL-CM5B-LR	Institut Pierre-Simon Laplace (IPSL)	Marti and others (2010)
M	MIROC-ESM-CHEM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies (MIROC)	Watanabe and others (2010)
N	MIROC-ESM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies (MIROC)	Watanabe and others (2010)
Ο	MIROC5	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies (MIROC), and Japan Agency for Marine-Earth Science and Technology	Watanabe and others (2010)
P	MRI-CGCM3	Meteorological Research Institute (MRI)	Yukimoto and others (2012)
Q	NorESM1-M	Norwegian Climate Centre (NCC)	Bentsen and others (2013)
R	bcc-csm1-1-m	Beijing Climate Center, China Meteorological Administration (BCC)	Xiao-Ge and others (2013)
S	bcc-csm1-1	Beijing Climate Center, China Meteorological Administration (BCC)	Xiao-Ge and others (2013)
T	inmcm4	Institute for Numerical Mathematics (INM)	Volodin and others (2010)

 $^{^{1}}Letters$ index the models and are used to identify panels in figures 3–6, 10–13, and 18–21.

Climate and Hydrology Context

Air Temperatures

For Plecoptera spp., increased temperatures are linked to shifts in distribution (Sheldon, 2012), increased physiological stress (Birrell and others, 2020), reduced reproductive success (Nebeker, 1971), and reduced survival through direct and indirect mechanisms (Hogg and Williams, 1996). This section investigates the current and future distribution of annual and summer mean temperatures. Historical trends are presented to contextualize the rate and magnitude of future changes.

Historical Warming and Elevation Gradients of Temperature

The southeastern United States is a warm region of the United States with a wide seasonal variation in annual maximum and minimum temperatures. During the 20th century, the southeastern United States has warmed less than the rest of the contiguous United States (Pan and others, 2004; Meehl and others, 2012; Mascioli and others, 2017; Vose and others, 2017; Partridge and others, 2018) including specifically in mountainous areas like the Great Smoky Mountains National Park (not shown) on the border of Tennessee and North Carolina (Lesser and Fridley, 2016). From 1901–60 to 1986–2016, average annual temperature in the southeastern United States increased by 0.3 °degree Celsius (°C), while annual average maximum and minimum temperatures increased by 0.1 °C and 0.4 °C, respectively (table 6.1 in Vose and others, 2017). Average annual temperatures in CONUS increased by 0.7 °C for the same time period, while annual average maximum and minimum temperatures increased by 0.6 °C and 0.8 °C, respectively (table 6.1 in Vose and others, 2017).

The annual mean temperature (defined as the air temperature at 2 m above ground) from 1979 to 2008 was 12.6 °C in the study area and ranged from less than 8 °C in the mountainous regions of West Virginia to greater than 16 °C in North Carolina (fig. 2A). Summer (June through August [JJA]) temperature average for the study area was 22.3 °C and ranged from 16 °C in West Virginia to 28 °C in Tennessee (fig. 2B). Monthly mean maximum temperature in the study area from 1979 to 2008 ranged from 7.4 °C in January to 29.2 °C in July (fig. 2E). Similarly, monthly mean minimum temperature in the study area ranged from -4.1 °C in January to 17.2 °C in July. The temperature distribution is aligned with elevation and latitude. In general, lower latitude areas are warmer than locations farther north, and temperature is negatively correlated with elevation. Table 2 contains historical averages for observed annual and JJA temperature across the three elevation bands highlighted in figure 1D.

Future Air Temperatures Will Be Warmer

Temperature is expected to rise in the study area throughout the 21st century in all emissions scenarios and climate model simulations. Absolute temperature change in the region is homogenous across elevations and follows a latitudinal gradient with northern areas warming more than southern areas. The southeastern United States region is projected to warm less than other areas in the contiguous United States at the same latitude, in keeping with historical trends (fig. 6.7 in Vose and others, 2017).

For the study domain in all models, all time periods, and both emissions scenarios, projections demonstrate that average annual and summer temperature will increase relative to the historical period (1971–2000). Summer mean temperatures will increase more than annual mean temperatures for each time period and emissions scenario. Average temperature changes for the study area in all time periods and emissions scenarios for the five-model sample are given in tables 3 and 4. The median model projects that annual mean temperatures will increase by 2.7 °C by the end of century (2070–99) under emissions scenario RCP4.5 (fig. 3) and by 4.7 °C under emissions scenario RCP8.5 (fig. 4). Similarly, summer temperatures are projected to increase in the median model by 3.0 °C under emissions scenario RCP4.5 (fig. 5) and by 5.3 °C under emissions scenario RCP8.5 (fig. 6). Although all models agree about the direction of change, there is still spread in the projected average magnitude of change, with larger model spread happening in the late 21st century (2070–99) and under the higher emissions scenario (RCP8.5) for annual and summer mean temperatures.

Model spread in projected temperature changes is wider for summer mean temperatures than for the annual mean. As seen in figure 7 and figure 8, this larger spread may be affected by a few models in the summer mean. Regardless, these outlier models are still plausible projections of future conditions and should be considered for possible risks to species and habitat. The full spread of annual temperature model projections by the end of century (2070–99) under RCP4.5 is 4.7 °C, ranging from an increase of 2.0 °C to an increase of 6.7 °C. Similarly, the full spread of model projections of summer temperature by the end of century (2070–99) under RCP8.5 is 6.0 °C, ranging from an increase of 2.3 °C to an increase of 8.3 °C.

Precipitation

Most Plecoptera spp., including *T. lobata*, *R. kirchneri*, and *A. kosztarabi*, rely on stream habitats for part of their lifecycle, likely making these species sensitive to changes in precipitation. Changes in precipitation seasonality and amount may lead to shifts in distribution (Shah and others, 2014), increased physiological stress, and reduced reproductive stress through habitat modification (Butler and others, 2015) and changes to food availability (Piano and others, 2020). Extreme precipitation events have the potential to reduce survival through contamination of waterways and landscape change. Without established species specific thresholds, this analysis focuses on annual and summer total precipitation and annual extreme events.

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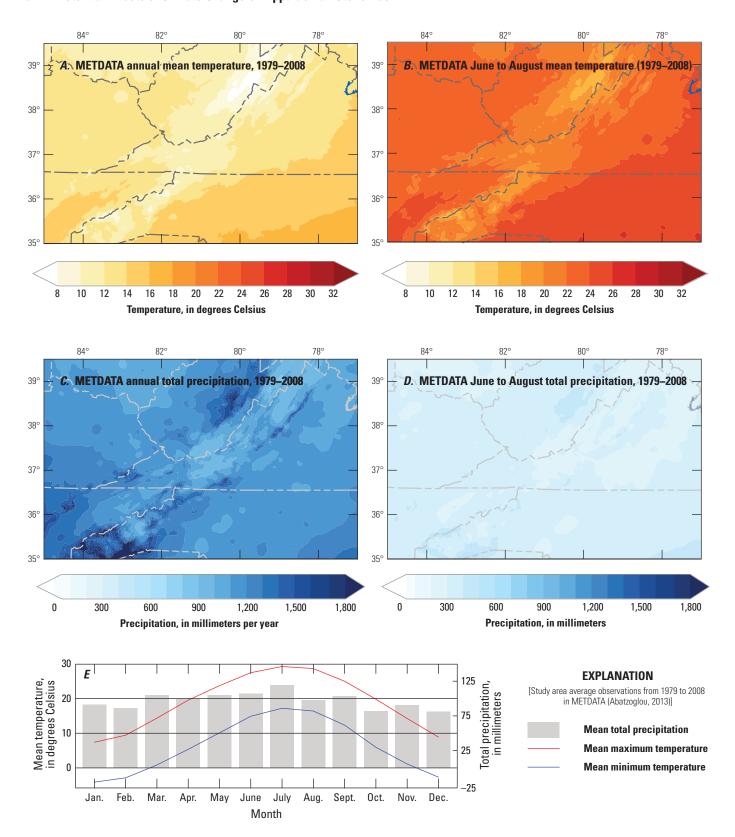


Figure 2. Historical (1979–2008) average of observations (gridMET/METDATA). *A*, annual average 2-meter air temperature, *B*, June through August (JJA) average 2-meter air temperature, *C*, annual average total precipitation, and, *D*, JJA average total precipitation, *E*, histogram of monthly average total precipitation, maximum temperature, and minimum temperature.

Table 2. Historical (1979–2008) study area (fig. 1*A*) and elevation band (fig. 1*D*) averages of annual and summer (June through August) mean temperature and total precipitation in gridMET/METDATA.

ſ°C. des	gree Celsius: JJ	A. June through	August: mm/ve	ar, millimeter p	er vear: mm/season	. millimeter per seas	son: <. less than: n	n, meter; >, greater than

Area	Annual mean air temperature (°C)	JJA mean air temperature (°C)	Annual total precipitation (mm/year)	JJA total precipitation (mm/season)	
Study area	12.6	22.3	1,168	324	
Elevation band 1: <450 m	13.7	23.6	1,145	315	
Elevation band 2: 450 m to <900 m	11.8	21.4	1,146	321	
Elevation band 3: >900 m	10.3	19.3	1,336	370	

Historical Wetting and Elevation Gradients of Precipitation

Precipitation in the region is spatially variable, highly affected by elevation, and exhibits little seasonal variation in the study area (fig. 2E). The average monthly total precipitation from 1979 to 2008 was 97.3 millimeter (mm); the monthly precipitation increases gradually from an average low of 81.2 mm in December to a high of 119.2 mm in July. This amounts to an average annual total precipitation of 1,168 mm with an average JJA total of 324 mm. Historical total precipitation exhibits a similar elevation pattern to temperature. The 900 m and above elevation band had an annual average total precipitation of 1,336 mm with the lower elevation bands each totaling roughly 1,145 mm. Table 2 contains historical averages for observed annual and JJA total precipitation across the three elevation bands highlighted in figure 1D. The overall study area is evenly balanced between winter/spring (January through May) and summer/autumn (June through October) precipitation, but mountainous areas in the south of the domain experience wetter winters/springs relative to drier summers/autumns.

Analyzing long-term historical trends in precipitation in this study area is difficult because of the lack of long-duration ground observations at high elevations and the large spatial heterogeneity of precipitation associated with complex topography. Satellite observations are increasingly able to capture precipitation totals in surface-data sparse regions, but their short period of record reduces the robustness of trend analysis. Lesser and Fridley (2016), in a study of high elevation weather stations (as much as 1,937 m) in the Great Smoky Mountains National Park, found a steady rise in precipitation through the 20th century. Annual precipitation from 1901-60 to 1986-2015 has been increasing west of the Appalachians and decreasing to the south and east (fig. 7.1 in Easterling and others 2017). By season, autumn precipitation increased uniformly across the region, whereas changes in winter, spring, and summer precipitation were mixed with the Appalachians being a transitional zone.

Increases in Extreme Precipitation Interact with Regional Topography

Past analysis of extreme precipitation indicates contrasting trends in the Appalachians and southeastern United States region. Differences stem partially from sparse data and differing thresholds and determinations of what constitutes an extreme event. Analysis of observed extreme precipitation for the southeastern United States region as a whole finds a 10.41-mm increase in the daily 20-year return level precipitation in autumn in the southeastern United States and Appalachians from 1901-60 to 1986-2015 (fig. 7.2 in Easterling and others, 2017). This increase is smaller in the winter and summer (3.81 and 2.29 mm, respectively) and in spring slightly decreases (-0.51 mm; fig. 7.2 in Easterling and others, 2017). Janssen and others (2014) found a positive trend in extreme precipitation events (2-day, 5-year, 10-year, and 20-year events) during the 20th century in the southeastern United States and specifically at weather stations in the south of the domain at the borders of Tennessee and North Carolina (figs. 4 and 6 in Janssen and others, 2014). Conversely, weather stations in the Appalachians tend toward fewer days with precipitation greater than 76.2 mm from 1950 to 2016 (fig. 19.3 in Carter and others, 2018) and a tendency towards fewer dry days and more days with light precipitation (Kinlaw and others, 2019). Skeeter and others (2019) found an increase in intense precipitation events (events in the 99th percentile of the record) from 1950 to 2016 in the Piedmont and Appalachian Highlands, but the trend was statistically insignificant (p-value=0.080 and p-value=0.066 relative to α =0.05; Skeeter and others, 2019).

Averaged across the study area, the 2-day total annual maximum precipitation has increased from 1979 to 2021 (fig. 9B). On average from 1979 to 2008 the 2-day annual maximum precipitation is larger in mountainous regions (fig. 9A). Conversely, the number of days with measurable precipitation (defined here as more than 1 mm) has decreased from 1979 to 2021 (fig. 9D). This increase in heavy precipitation events and decrease in precipitation days is consistent with the trend in average precipitation totals during this period.

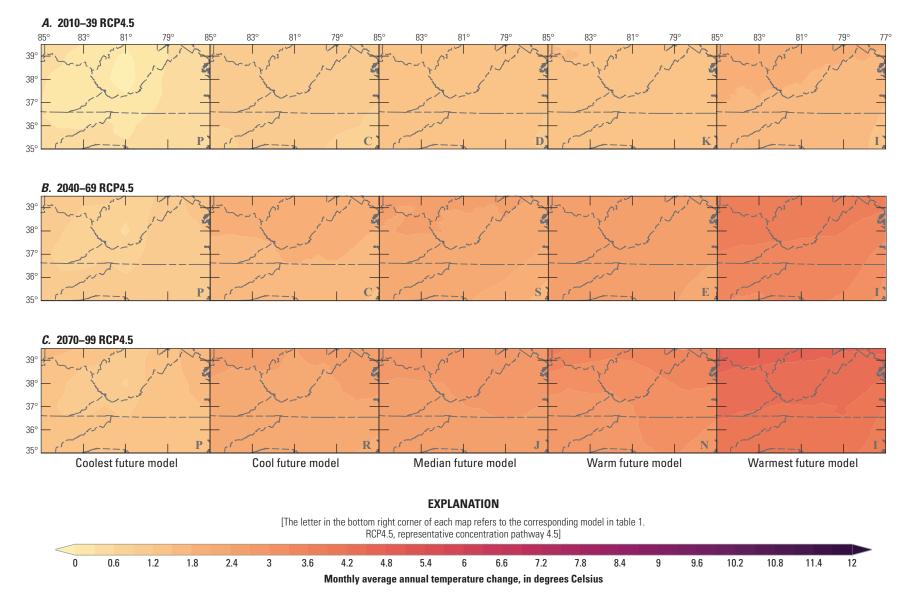


Figure 3. Downscaled climate simulations under emissions scenario representative concentration pathway 4.5 showing annual mean 2-meter air temperature change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

Table 3. Study area average of change in annual mean 2-meter temperature for the selected models for the three future time periods under representative concentration pathway 4.5 and representative concentration pathway 8.5 using MACAv2-METDATA downscaled global climate model data (Abatzoglou and Brown, 2012).

[RCP, representative concentration pathway]

Model	RCP4.5			RCP8.5				
	2010–39	2040–69	2070–99	2010–39	2040-69	2070–99		
Coolest future	+0.3	+0.9	+1.3	+0.3	+1.5	+2.6		
Cool future	+1.0	+1.8	+2.3	+1.1	+2.6	+4.1		
Median future	+1.3	+2.3	+2.7	+1.4	+2.8	+4.7		
Warm future	+1.4	+2.5	+3.1	+1.5	+3.2	+5.1		
Warmest future	+1.8	+3.5	+4.2	+2.0	+4.3	+6.7		

Table 4. Study area average of change in summer (June through August) mean 2-meter temperature for the selected models for the three future time periods under representative concentration pathway 4.5 and representative concentration pathway 8.5 using MACAv2-METDATA downscaled global climate model data (Abatzoglou and Brown, 2012).

[RCP, representative concentration pathway]

Model		RCP4.5		RCP8.5				
	2010–39	2040–69	2070–99	2010–39	2040–69	2070-99		
Coolest future	+0.5	+1.0	+1.6	+0.5	+1.9	+2.9		
Cool future	+1.0	+1.9	+2.4	+1.1	+2.8	+4.6		
Median future	+1.3	+2.5	+3.0	+1.5	+3.3	+5.3		
Warm future	+1.5	+2.7	+3.3	+1.8	+3.4	+5.7		
Warmest future	+2.2	+4.0	+4.8	+2.3	+5.6	+8.3		

Mixed Projections of Future Precipitation Totals

Precipitation changes in this region are projected to be more heterogenous than temperature in their spatial pattern and temporal trends. There is also more spread in the model projections and less agreement among models on whether precipitation will increase or decrease. The difficulty of projecting future precipitation in general has been noted (Shepherd, 2014) and supported by the Fourth National Climate Assessment. The Fourth National Climate Assessment shows increases in average model mean precipitation across all seasons in the southeastern United States. Increases in winter and spring precipitation are shown to be large in comparison to natural variability whereas increases in the summer and autumn are small in comparison to natural variability (fig. 7.5 in Easterling and others, 2017). Stronger increases in some seasons have the potential to shift precipitation distributions or create a more defined precipitation seasonality in an area with little historical seasonality like the study area.

Projections of annual total precipitation indicate a large spread for models under emissions scenarios RCP4.5 and RCP8.5. More models indicate precipitation amounts will generally be greater, but several plausible models indicate future precipitation for the study area and areas in

the northwestern part of the domain could be lower than the historical period (figs. 10 and 11). Reductions in annual total precipitation are limited mainly to areas west of the Appalachians in both emissions scenarios. This pattern also is seen in the projections of summer precipitation change, although some models project drying across the whole domain (figs. 12 and 13). The pattern is generally consistent with that presented in Fernandez and Zegre (2019).

However, in this analysis the median model averaged across the study area shows consistent increases in annual and JJA precipitation for all time periods and emissions scenarios whereas the analysis of mean model change in Fernandez and Zegre (2019) shows a changing direction in the precipitation trend throughout the 21st century under both emissions scenarios. Average precipitation changes for the study area in all time periods and emissions scenarios are given in tables 5 and 6.

The spread in precipitation at mid-century (2040–69) is higher in RCP4.5 than RCP8.5 in annual and summer precipitation. By the end of the century (2070–99) this reverses and the spread in precipitation is higher in RCP8.5 than RCP4.5 in the annual and summer total precipitation. In all time periods the spread in summer precipitation projections is larger than for annual precipitation.

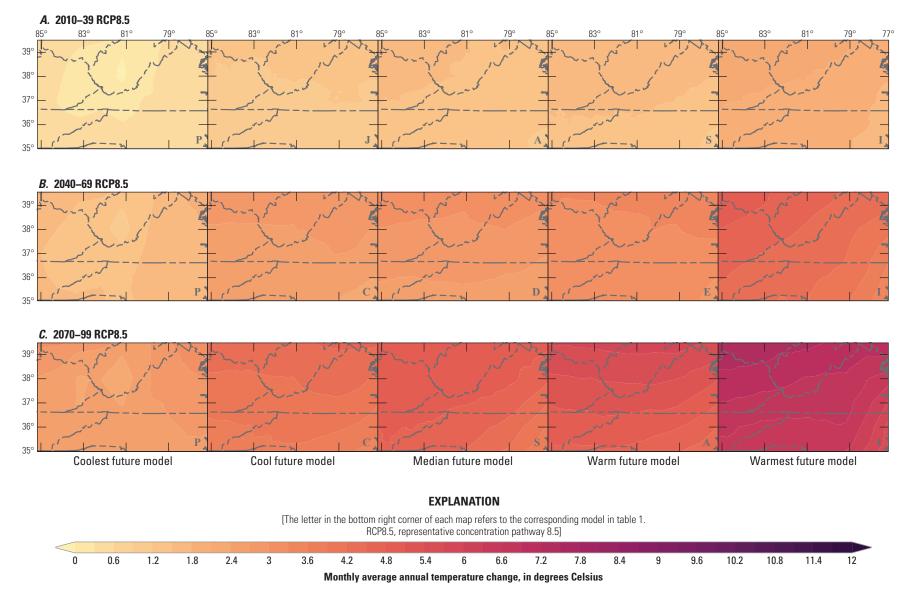


Figure 4. Downscaled climate simulations under emissions scenario representative concentration pathway 8.5 showing annual mean 2-meter air temperature change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

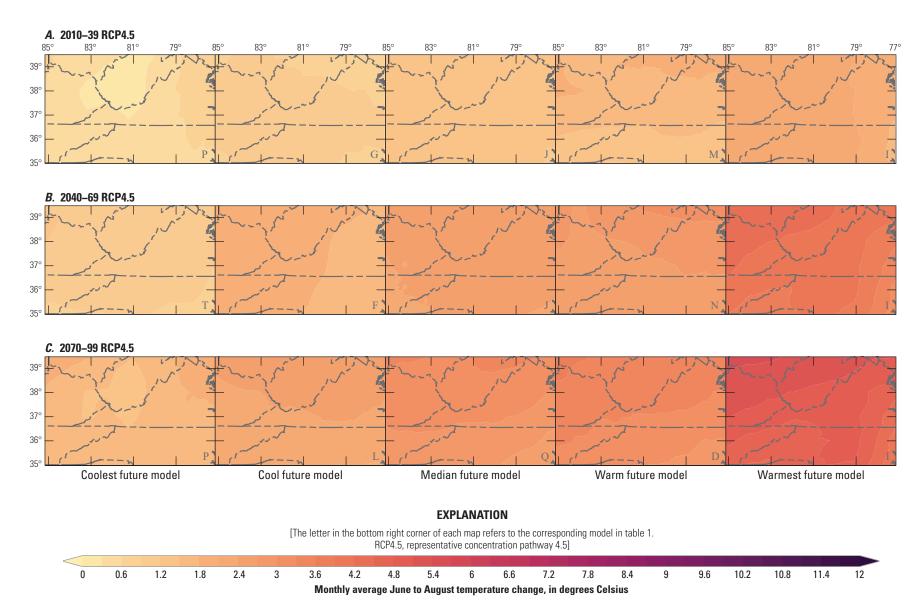


Figure 5. Downscaled climate simulations under emissions scenario representative concentration pathway 4.5 showing summer (June through August) mean 2-meter air temperature change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

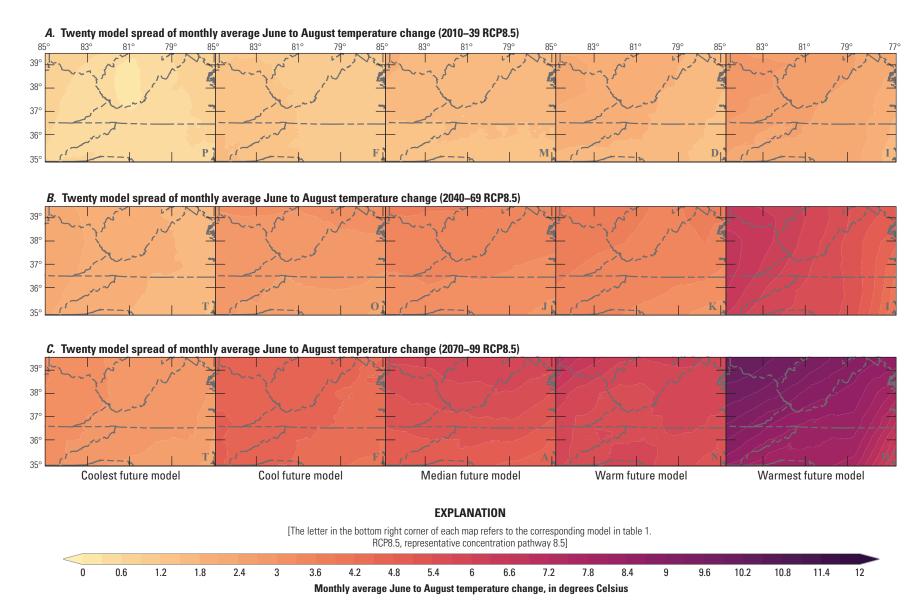
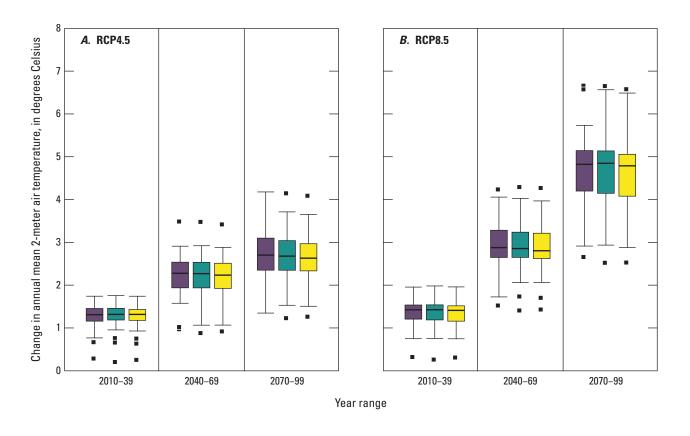


Figure 6. Downscaled climate simulations under emissions scenario representative concentration pathway 8.5 showing summer (June through August) mean 2-meter air temperature change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.



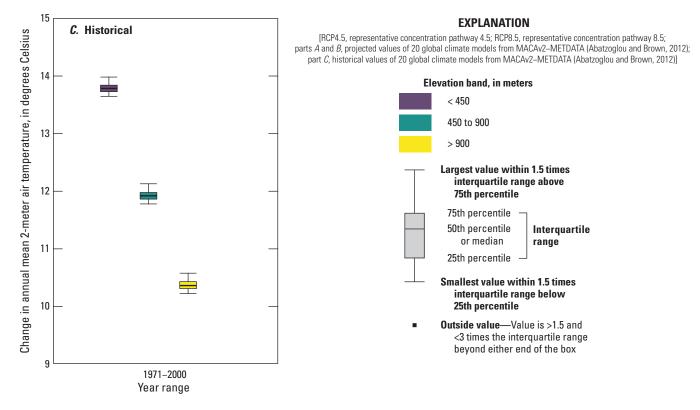


Figure 7. Downscaled climate simulations showing annual mean 2-meter air temperature change from the historical period (1971–2000) to the early (2010–39), mid (2040–69), and late (2070–99) 21st century under, *A*, emissions scenario representative concentration pathway 4.5, *B*, emissions scenario representative concentration pathway 8.5, and, *C*, the historical (1971–2000) value in the downscaled climate simulations.

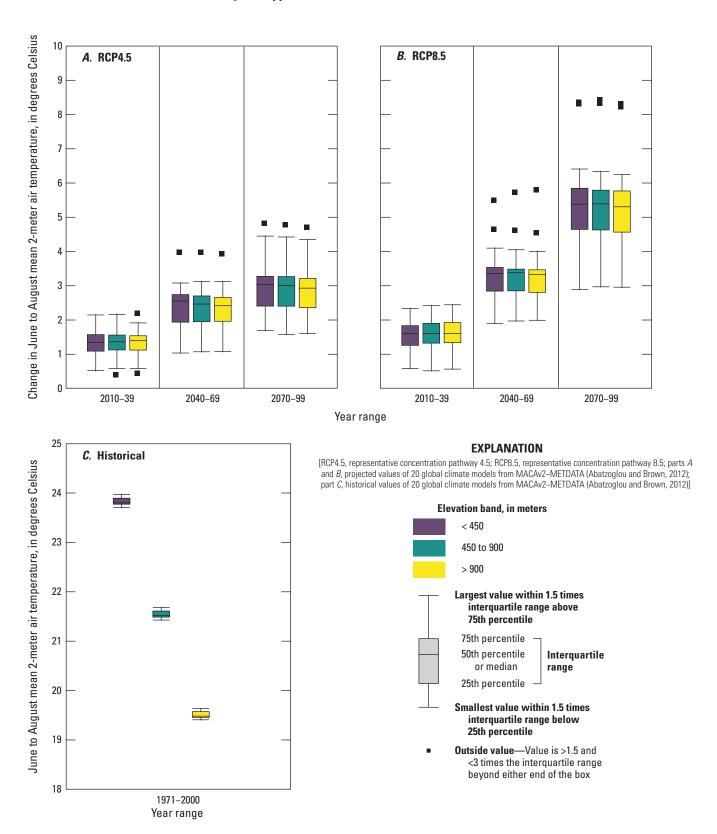


Figure 8. Downscaled climate simulations showing summer (June through August) mean 2-meter air temperature change from the historical period (1971–2000) to the early (2010–39), mid (2040–69), and late (2070–99) 21st century under, *A*, emissions scenario representative concentration pathway 4.5, *B*, emissions scenario representative concentration pathway 8.5, and, *C*, the historical (1971-2000) value in the downscaled climate simulations.

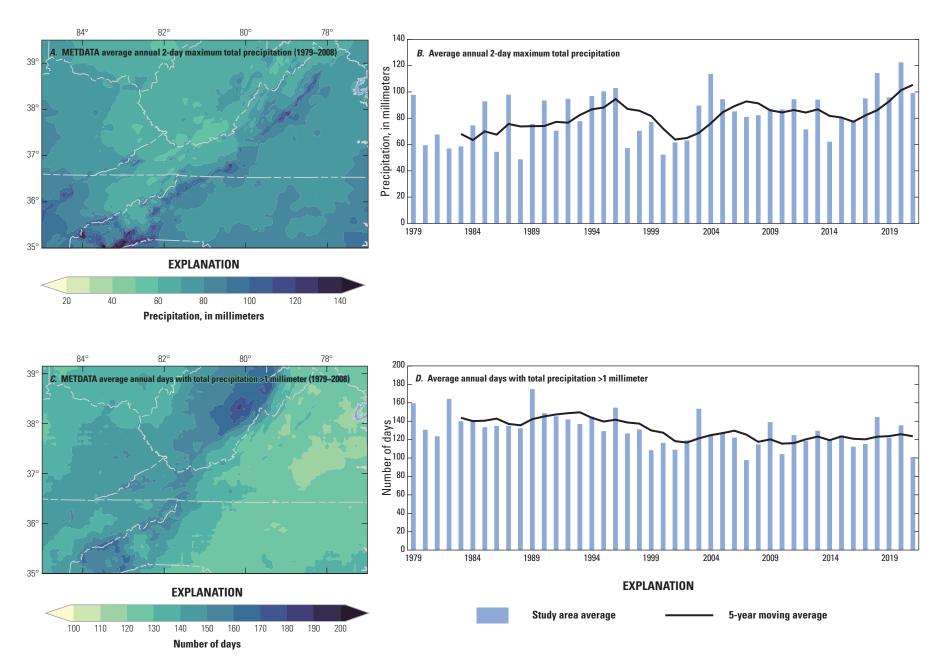


Figure 9. Extreme precipitation events over the domain and study area in the observations (gridMET/METDATA), with, *A*, 1979–2008 period average annual maximum 2-day total precipitation, *B*, Yearly study area average annual maximum 2-day total precipitation for 1979–2021, *C*, 1979–2008 period average annual days with total precipitation greater than 1 millimeter, and, *D*, Yearly study area average annual days with total precipitation greater than 1 millimeter for 1979–2021.

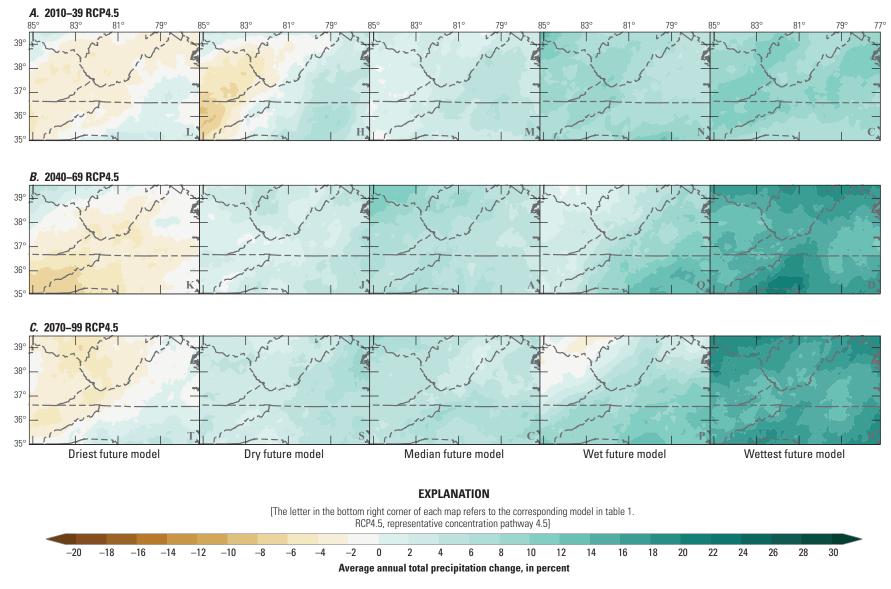


Figure 10. Downscaled climate simulations under emissions scenario representative concentration pathway 4.5 showing annual total precipitation change from the historical period (1971–2000) to the, A, early (2010–39), B, mid (2040–69), and, C, late (2070–99) 21st century.

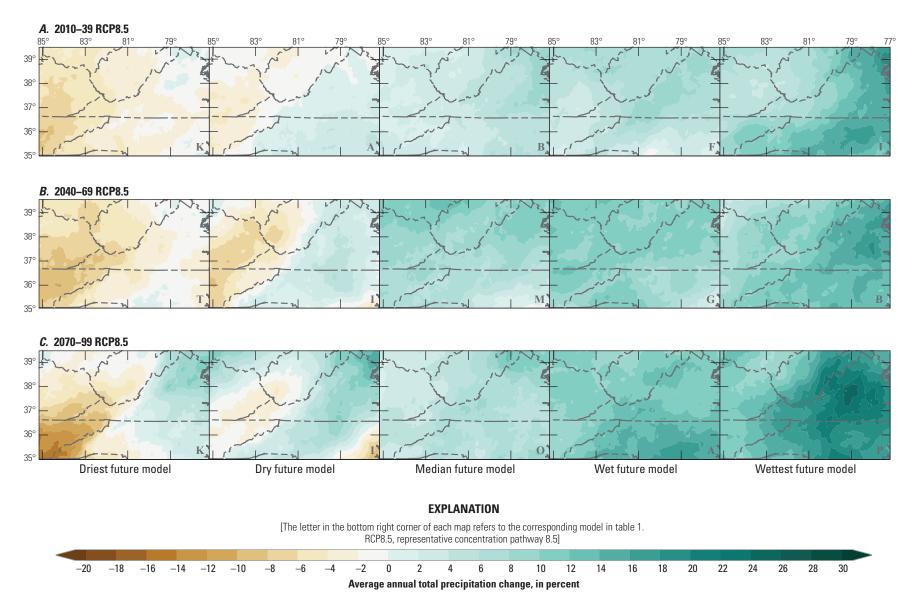


Figure 11. Downscaled climate simulations under emissions scenario representative concentration pathway 8.5 showing annual total precipitation change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

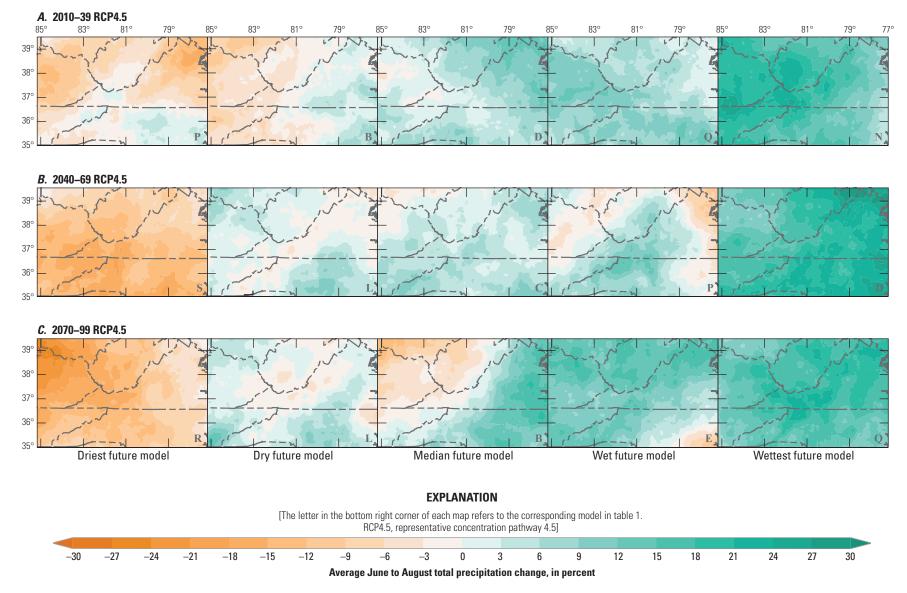


Figure 12. Downscaled climate simulations under emissions scenario representative concentration pathway 4.5 showing summer (June through August) total precipitation change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

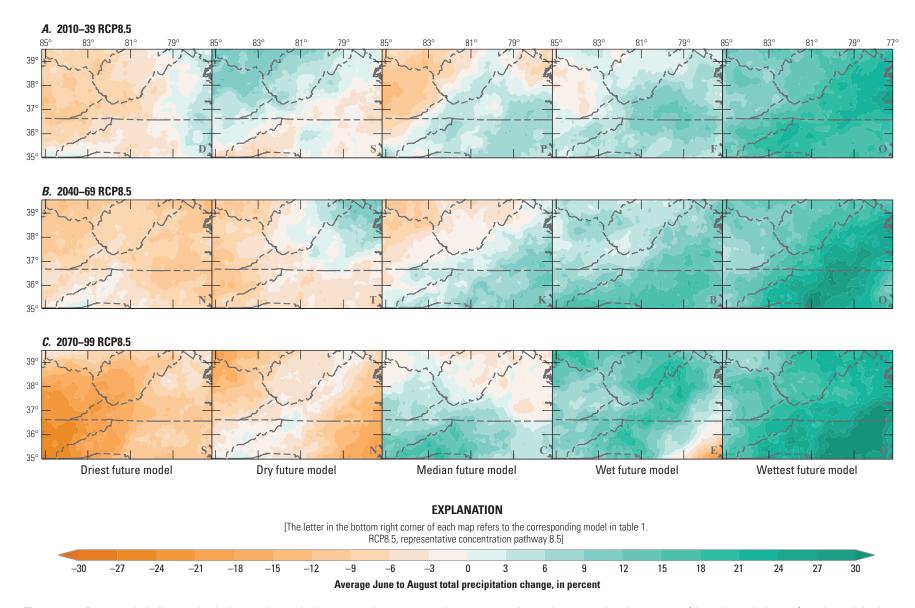


Figure 13. Downscaled climate simulations under emissions scenario representative concentration pathway 8.5 showing summer (June through August) total precipitation change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

Table 5. Study area average of change in annual total precipitation from the historical period for the selected models for the three future time periods under representative concentration pathway 4.5 and representative concentration pathway 8.5 using MACAv2-METDATA downscaled global climate model data (Abatzoglou and Brown, 2012).

	concentration				

Model	RCP4.5			RCP8.5		
	2010–39	2040–69	2070–99	2010–39	2040–69	2070–99
Driest future	-1.9	-3.4	-1.6	-2.6	-4.3	-0.6
Dry future	+1.9	+1.8	+4.1	+0.8	+1.8	+4.0
Median future	+4.2	+5.5	+6.1	+3.9	+7.2	+6.6
Wet future	+7.1	+7.9	+8.9	+7.4	+9.7	+12.9
Wettest future	+10.0	+16.1	+15.0	+10.3	+13.0	+19.6

Table 6. Study area average of change in summer (June through August) total precipitation from the historical period for the selected models for the three future time periods under representative concentration pathway 4.5 and representative concentration pathway 8.5 using MACAv2-METDATA downscaled global climate model data (Abatzoglou and Brown, 2012).

[RCP, representative concentration pathway; – or +, percent change from historical period]

Model	RCP4.5			RCP8.5		
	2010–39	2040–69	2070–99	2010–39	2040–69	2070–99
Driest future	-2.9	-14.0	-12.2	-4.4	-6.3	-14.4
Dry future	-0.2	+0.2	+0.7	-1.0	-2.2	-3.4
Median future	+4.0	+5.1	+4.9	+3.7	+3.9	+7.2
Wet future	+7.9	+9.5	+11.3	+9.3	+10.5	+15.9
Wettest future	+17.9	+20.0	+19.1	+19.0	+22.6	+22.7

Although the historical precipitation at higher elevations (greater than [>] 900 m) is greater than at lower elevations (figs. 14 and 15), the projected absolute change is small relative to the overall total. Notably, higher elevations see a larger spread in the model projected future conditions in the annual total and summer total precipitation for both emissions scenarios. This elevation difference likely highlights the strong effect that terrain has on precipitation and the difficulty of capturing these processes in model simulations.

Climate models have been documented to underestimate extreme precipitation in the southeastern United States in the historical period, especially after the 1980s with observed extreme events exceeding the full model spread of historical simulations (Janssen and others, 2014). The drivers of variation among models and the individual model ensembles are not fully understood, and results can also be affected by downscaling and bias correction methodology (Wang and others, 2020). Future precipitation is expected to become more intense based on thermodynamic principles (Easterling and others, 2017), and a potential component of increased precipitation in the region will be from hurricanes and similar tropical storms (Wright and others, 2015).

Runoff and Streamflow

Plecoptera spp. are likely sensitive to changes in runoff and resulting streamflow, which alter stream habitats, water availability, and dissolved-oxygen concentration. Decreases in streamflow can lead to distribution changes (Datry and others, 2011), reduced reproductive success (Piano and others, 2020), and reduced survival (Smith and others, 2003). Like precipitation, the lack of species-specific research restricts this analysis to annual and summer total runoff.

Historical Streamflow Trends Differ by Elevation in this High Base Flow, **Cool Water Region**

The high elevation regions of the Appalachians serve as headwaters for the surrounding low-lying areas and are sustained by higher precipitation as well as groundwater availability (Boettner and others, 2014). Streams in the domain fall into three main classifications as described in McManamay and others (2014). High elevation streams in the southeast Appalachian range are largely classified as stable high base flow with high base flows and moderately high runoff. Streams in the surrounding lower elevation

regions are classified mainly as perennial, with lower base flow and more variability from a winter/spring high flow to a summer/autumn low flow (McManamay and others, 2014; McManamay and DeRolph, 2019). The 8-digit Hydrologic Units identified as part of the study area are all classified as dominantly stable high base flow and three of the 8-digit Hydrologic Units have a secondary perennial classification (06010101, 06010108, and 02080203; McManamay and others, 2013). This stability and high base flow will likely continue providing habitat for species lacking adaptations for intermittent flow under future runoff reductions. The thermal regimes of these streams range from variable cool (annual maximum water temperature from 20 to 28 °C; mean annual water temperature amplitude of 11.0 °C) to variable cold (annual maximum water temperature below 20 °C; mean annual water temperature amplitude of 9.2 °C). Temperatures differ by elevation with a moderate diurnal range of summer stream temperature (2.2–4.6 °C; Maheu and others, 2016; McManamay and DeRolph, 2019).

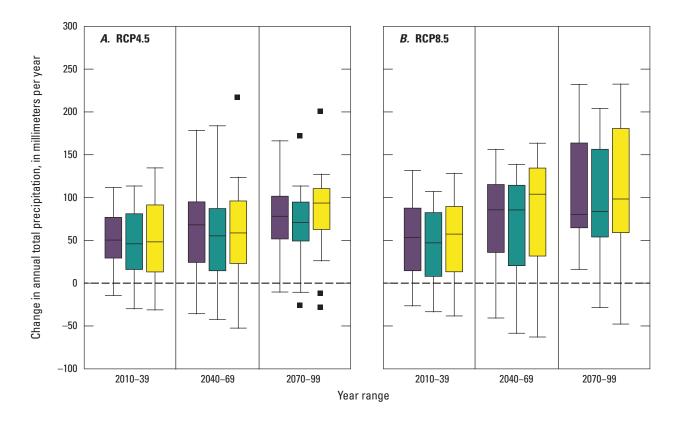
The trends in average streamflow in the region have been mixed during the historical period but have skewed towards decreases especially later in the 20th century. Gages in the southwest of the study area range from -20 percent to +20 percent mean annual streamflow from 1940 to 2018 and, gages in the northeast decreased by 20 percent to more than 50 percent (U.S. Geological Survey, 2020). The decrease has been even more uniform from the 1960s, though trends are largely insignificant (using Mann-Kendall p-value less than [<] 0.05; fig. 8 in Dudley and others, 2020). Sadeghi and others (2019) found that streamflow decreased in the southeastern United States in the last 25 years among 26 unimpaired streamgages. Trends in gages in the study area are largely significant at the α =0.10 level (fig. 3 in Sadeghi and others, 2019). The 7-day low streamflow has decreased in the southeastern United States including the Appalachians when trends are calculated from the mid-century, again with trends in the Appalachians being insignificant at the α =0.05 level (fig. 2 in Dudley and others, 2020). High flow changes have been more mixed. Although annual peak streamflow has largely decreased in the Appalachians, Hodgkins and others (2019) found an increase in the number of 5-year events from 1941 to 2015 in some parts of the study area with trends meeting the study's Mann-Kendall significance threshold (p-value<0.05; figs. 4 and 7 in Hodgkins and others, 2019).

Higher elevations (>900 m) have much greater runoff as compared to lower elevations in the historical simulations of MACAv2-METDATA (figs. 16B and 17B). Areas above 900 m elevation average 650 mm of annual total runoff as compared to 350–450 mm in the lower elevation bands. A similar gap exists in summer total runoff; areas above 900 m elevation average 90 mm as compared to 40–55 mm in the lower elevation bounds. While the summer season (June through August) produces nearly a quarter of the annual total precipitation, the runoff proportion is much smaller because of higher temperatures and consequently higher evapotranspiration.

Mixed Projections of Future Runoff Totals

Runoff projections are directly connected to projected changes in precipitation and increases in evaporative demand associated with higher temperatures. Under future climate projections, temperature changes are negatively correlated with runoff changes and precipitation changes are positively correlated with runoff changes. The relations between temperature and precipitation to runoff are statistically significant but there is no significant correlation between temperature change and precipitation changes in models for the study area. Whereas the model spread in precipitation shifts toward an increase in precipitation through time, the runoff projections tend toward a decrease through time; nevertheless, the full spread of model projections is still broad, with some models projecting lower runoff and some models projecting higher runoff totals.

Reductions in annual total runoff happen mostly in areas west of the Appalachians in both emissions scenarios (figs. 18 and 19). The summer runoff projections are more spatially heterogenous and even the wettest model projects a decrease in summer total runoff in the north of the domain at the end of century under emissions scenario RCP8.5 (figs. 20 and 21). This is likely driven by the strong warming in the north of the domain that increases with time and under higher emissions scenarios. Overall, the median model averaged across the study area shows consistent decreases in annual and JJA runoff for all time periods and emissions scenarios (except summer runoff change in mid-century under RCP4.5). Average runoff changes for the study area in all time periods and emissions scenarios are given in tables 7 and 8. Note that in all time periods and emissions scenarios the model spread spans zero.



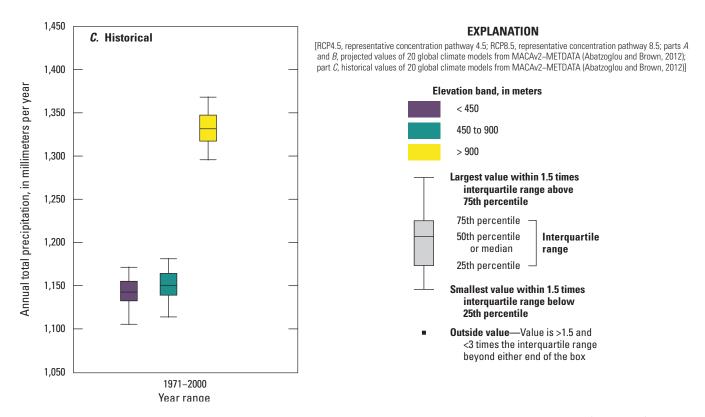
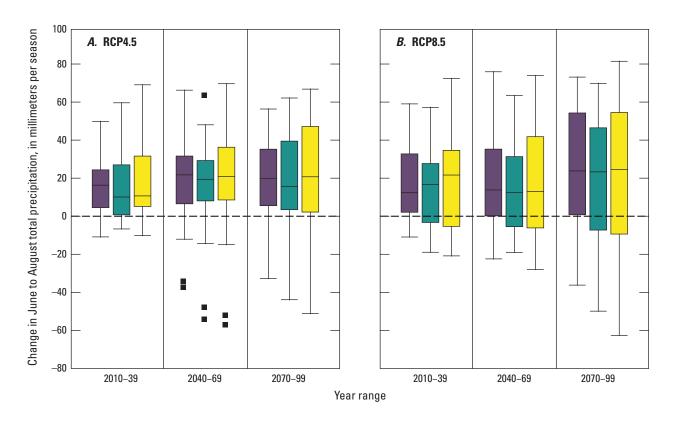


Figure 14. Downscaled climate simulations showing annual total precipitation change from the historical period (1971–2000) to the early (2010–39), mid (2040–69), and late (2070–99) 21st century under, *A*, emissions scenario representative concentration pathway 4.5, *B*, emissions scenario representative concentration pathway 8.5, and, *C*, the historical (1971-2000) value in the downscaled climate simulations.



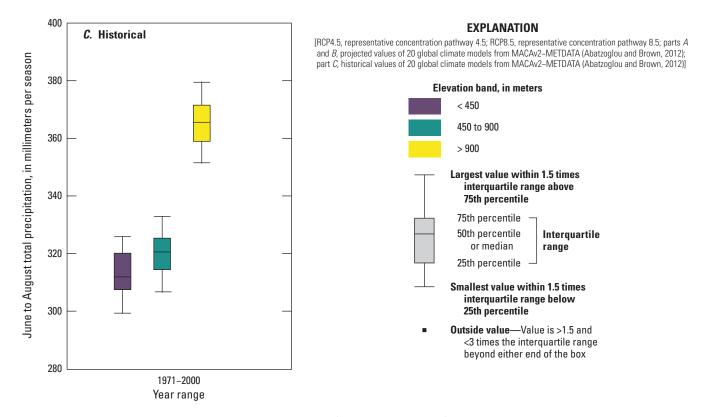
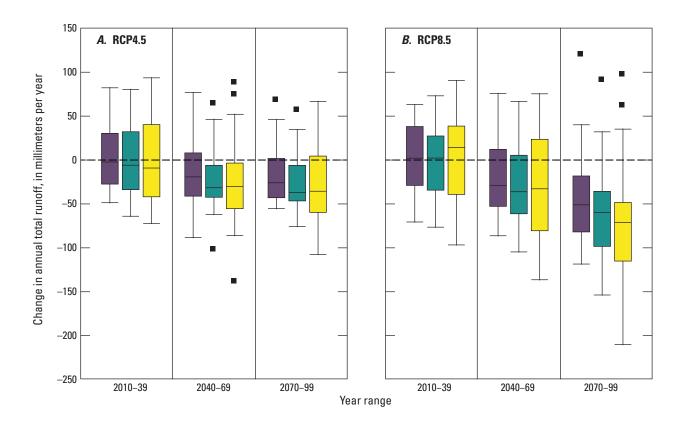


Figure 15. Downscaled climate simulations showing summer (June through August) total precipitation change from the historical period (1971–2000) to the early (2010–39), mid (2040–69), and late (2070–99) 21st century under, *A*, emissions scenario representative concentration pathway 4.5, *B*, emissions scenario representative concentration pathway 8.5, and, *C*, the historical (1971-2000) value in the downscaled climate simulations.



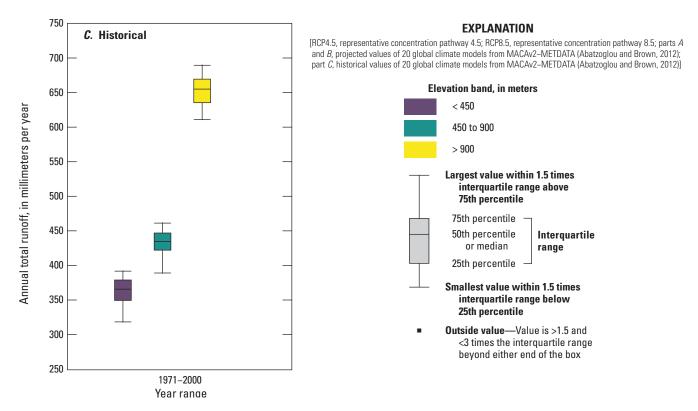
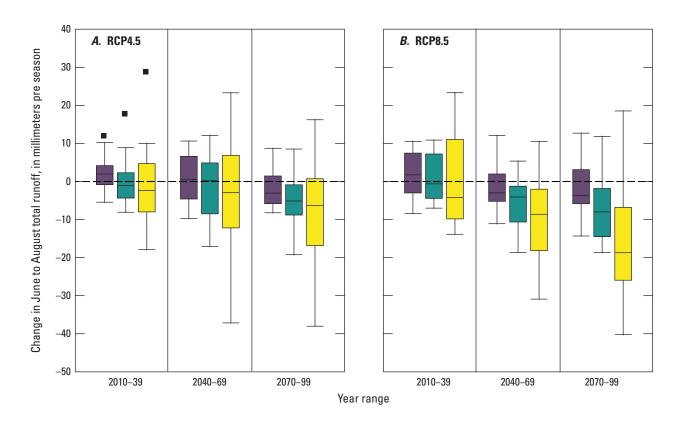


Figure 16. Downscaled climate simulations showing annual total runoff change from the historical period (1971–2000) to the early (2010–39), mid (2040–69), and late (2070–99) 21st century under, *A*, emissions scenario representative concentration pathway 4.5, *B*, emissions scenario representative concentration pathway 8.5, and, *C*, the historical (1971-2000) value in the downscaled climate simulations.



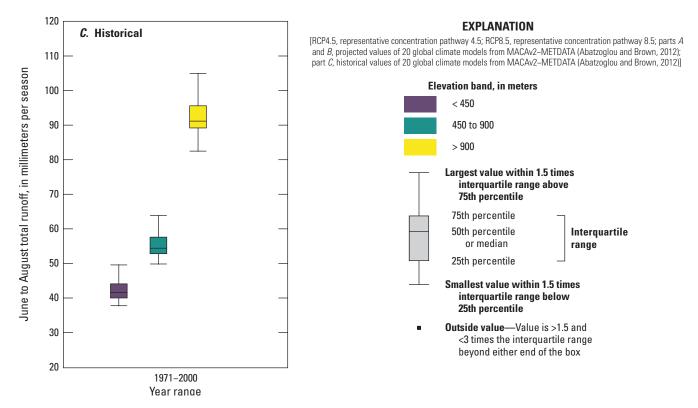


Figure 17. Downscaled climate simulations showing summer (June through August) total runoff change from the historical period (1971–2000) to the early (2010–39), mid (2040–69), and late (2070–99) 21st century under, *A*, emissions scenario representative concentration pathway 4.5, *B*, emissions scenario representative concentration pathway 8.5, and, *C*, the historical (1971-2000) value in the downscaled climate simulations.

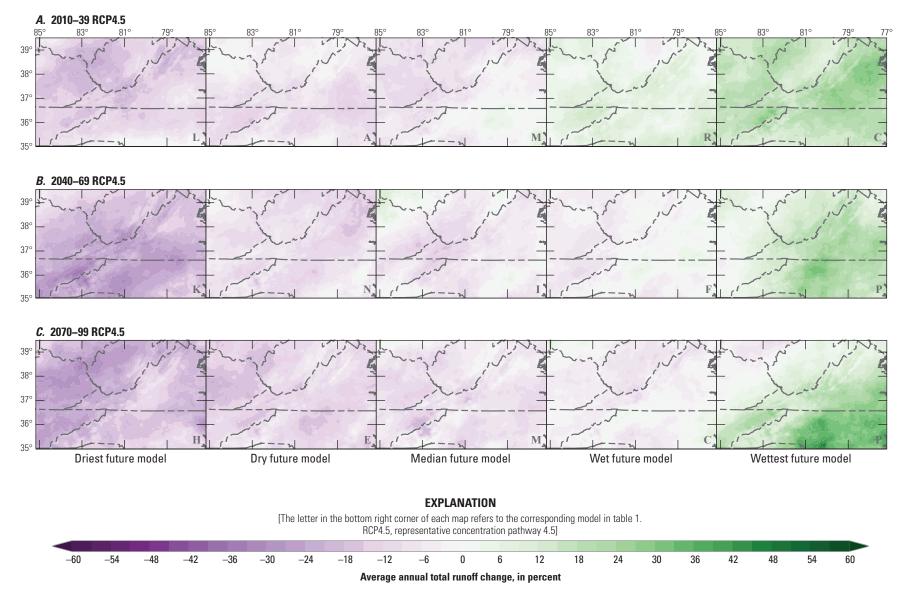


Figure 18. Downscaled climate simulations under emissions scenario representative concentration pathway 4.5 showing annual total runoff change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

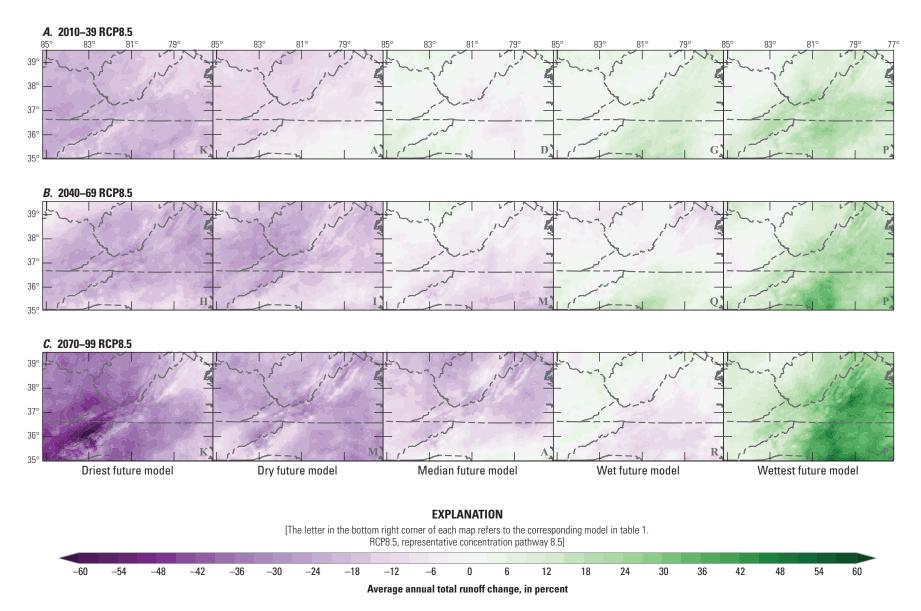


Figure 19. Downscaled climate simulations under emissions scenario representative concentration pathway 8.5 showing annual total runoff change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

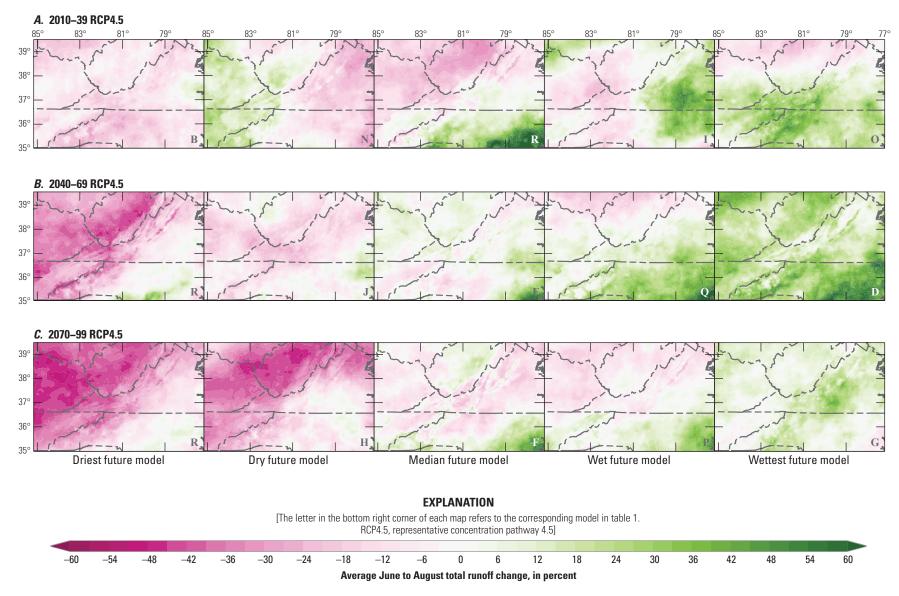


Figure 20. Downscaled climate simulations under emissions scenario representative concentration pathway 4.5 showing summer (June through August) total runoff change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

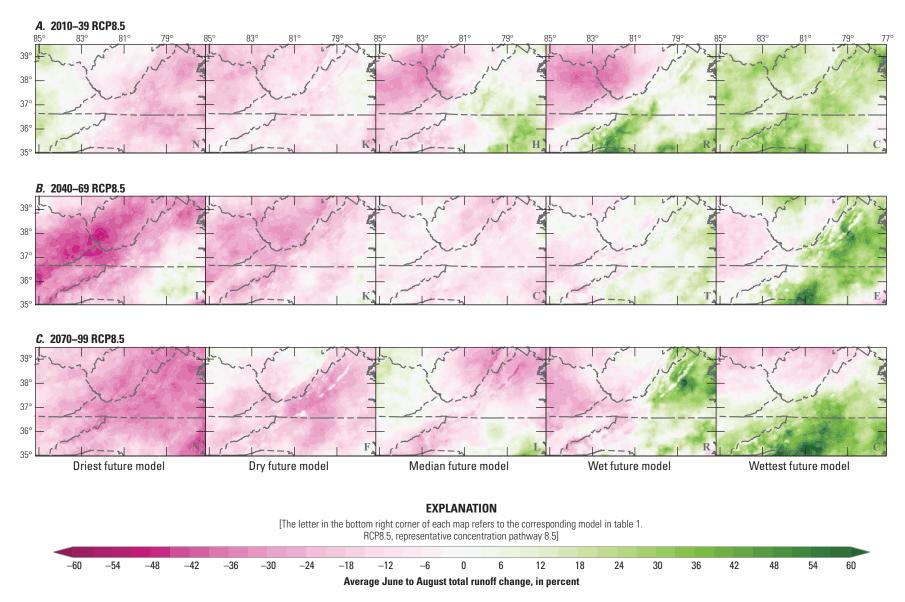


Figure 21. Downscaled climate simulations under emissions scenario representative concentration pathway 8.5 showing summer (June through August) total runoff change from the historical period (1971–2000) to the, *A*, early (2010–39), *B*, mid (2040–69), and, *C*, late (2070–99) 21st century.

Table 7. Study area average of change in annual total runoff from the historical period for the selected models for the three future time periods under representative concentration pathway 4.5 and representative concentration pathway 8.5 using MACAv2-METDATA downscaled global climate model data (Abatzoglou and Brown, 2012).

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Medel	RCP4.5			RCP8.5		
Model —	2010–39	2040–69	2070–99	2010–39	2040–69	2070–99
Driest future	-13.9	-23.3	-15.5	-18.2	-22.4	-33.6
Dry future	-8.7	-10.2	-11.3	-8.6	-18.2	-23.0
Median future	-2.7	-7.6	-8.0	-0.9	-8.2	-13.4
Wet future	+7.5	+0.0	-1.6	+8.1	+2.2	-6.7
Wettest future	+21.5	+20.3	+18.5	+18.2	+20.6	+30.7

Table 8. Study area average of change in summer (June through August) total runoff from the historical period for the selected models for the three future time periods under representative concentration pathway 4.5 and representative concentration pathway 8.5 using MACAv2-METDATA downscaled global climate model data (Abatzoglou and Brown, 2012).

[RCP, representative concentration pathway; - or +, percent change from historical period]

Madal	RCP4.5			RCP8.5		
Model	2010–39	2040–69	2070–99	2010–39	2040-69	2070-99
Driest future	-14.7	-20.4	-26.1	-15.2	-26.1	-32.7
Dry future	-4.4	-13.5	-13.9	-9.2	-15.9	-23.6
Median future	+1.7	+0.5	-8.3	+1.2	-8.0	-11.9
Wet future	+6.4	+13.6	-0.6	+14.2	+1.0	+3.9
Wettest future	+28.5	+22.4	+17.3	+22.2	+18.7	+27.2

Additional Climate Effects

Plecoptera spp. are likely sensitive to changes in air temperature, precipitation, and runoff mediated through changes to stream temperature, stream conditions, and land cover changes. We identify likely future changes to streams and land cover resulting from climate change within the distributions of *Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata*.

Stream Temperatures Likely to Warm with Increased Air Temperature and Reduced Runoff

Changing stream temperature is a primary effect of changing climate on stonefly habitat. Stream temperature is affected by several factors including air temperature, net radiation, flow rate, groundwater connectivity, drainage basin area, and shading from riparian vegetation (Constantz, 1998; Hill and others, 2014; Snyder and others, 2015; Trimmel and others, 2018). From 1960 to 2014, stream temperatures have increased by 1.1–2.2 °C at streamgages in southern and eastern Virginia (Jastram and Rice, 2015). Projected reductions in flow rate and increases in air temperature will likely increase stream temperatures in stonefly habitat locations for

the three species of focus in this report. Hill and others (2014) find that summer stream temperatures will increase under climate change in the southern Appalachians though at a lower rate than the contiguous United States-wide average.

Although stream temperature projections for the range of model projections and time periods are currently unavailable in the region of interest, fundamental climate drivers of stream temperature can inform likely directions of change. Constantz (1998) documented a strong coupling between streamflow and stream temperature on a daily basis in Colorado Rocky streams where low streamflow boosts afternoon stream temperatures, and these increased temperatures promote further streamflow loss. Higher streamflow also reduces the amplitude of diurnal stream temperature, which can lead to a smaller diurnal variation in dissolved oxygen content. This same relation between diurnal stream temperature variation and flow is found in Trimmel and others (2018), although they note that vegetation shading of the stream can dampen this relation. Trimmel and others (2018) found that stream shading in a strongly anthropogenically affected drainage basin under an extreme hot/dry climate scenario could reduce water temperature under climate change. Under a vegetation removal scenario, the daily maximum temperature of 20-year heat events at the end of the century increased by 4.5 °C (150-percent increase under status quo vegetation); conversely, adding additional vegetation cover mitigated this rise to 1.1 °C (30-percent increase under status quo vegetation; Trimmel and others, 2018). The study describes the effect of vegetation on stream temperature, though vegetation cover cannot mitigate all the increase in stream temperature under climate change.

Wildfire Risk Increases, but Remains Comparatively Lower

Fire risk is becoming an increasing concern under warmer average temperatures and reductions in relative humidity. The relative fire risk will increase in the Appalachians in the future under high emissions scenarios, but the absolute fire probability remains lower than the surrounding regions in the eastern and southern United States (Gao and others, 2021). The eastern Appalachian region has a 50- to 75-percent increase in annual fire probability from the baseline (1971–2000) to late century (2070–99) under RCP8.5 (Gao and others, 2021). The western region has a 75- to 100-percent increase in annual fire probability for the same period and emissions scenario.

Sedimentation, Contaminant Concentrations, and Landslides Increase with More Intense Rainfall

Changes in precipitation, including extreme precipitation, will likely affect the rates of sedimentation into streams and the occurrence of landslides and debris flows. Additionally, changes in the volume and timing of runoff and streamflow will modify inputs into the stream networks and may change contaminant concentrations. Wieczorek and Morgan (2008) studied the debris flow and landslide prone region of the central and southern Appalachian Mountains (not shown) and their connections to rain pulses from hurricanes, cloudbursts, and thunderstorms. Most of the species' distribution for Remenus kirchneri and Tallaperla lobata is in the moderatehigh incidence range for debris flows (Wieczorek and Morgan, 2008). The rate of rainfall is a critical factor in initiating debris flows but how that combines with total rainfall volume, antecedent conditions, and local geology is highly site specific. It is likely that higher intensity rainfall coupled with higher overall precipitation would increase the probability of landslide events in this region.

Ecological Context

Distribution

Most Plecoptera Species Inhabit Narrow Environmental Niches

Plecoptera spp. are generally assumed to have narrow thermal tolerances corresponding to restricted distributions in streams with certain flow and temperature conditions (Hotaling and others, 2020) (table 9). In experimental manipulations, larval growth, survival, and development are highly dependent on optimal temperature conditions (Sweeney and others, 1986); adult longevity also decreases with increasing temperature (Collier and Smith, 2000). In a stream warming manipulation, density of Plecoptera spp. decreased with increasing temperatures (Hogg and Williams, 1996). Experimental studies, while small in scope (Hotaling and others, 2020), support the hypothesis that Plecoptera spp. have narrow thermal tolerances relating to physiological stress and reproductive success (explored in subsequent sections).

There are no studies directly quantifying the environmental tolerances of the three Appalachian stoneflies: *Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata*. Based on most recently observed distributions (Verdone and Kondratieff, 2018) and projected changes in temperature, narrow ranging *T. lobata* and *R. kirchneri* are more likely to be affected by changing stream conditions. Future climate within the distributions of these species is likely to be outside of the range of historically experienced climate.

Suitable Plecoptera Habitat May Shift Up in Elevation or Latitude

Because of these narrow environmental tolerances, climate change is likely to spatially shift Plecoptera species' suitable niches higher in elevation or north in latitude. Based on bioclimatic envelope modeling using climate change projections, Plecoptera genera are predicted to have the largest latitudinal shift of any macroinvertebrates in North America (Shah and others, 2014). For some species of Plecoptera, studies have already documented contemporary elevational shifts in distribution (Sheldon, 2012). Poor historical sampling and concurrent changes to water quality and forest cover make it difficult to quantify distributional shifts caused by changes in climate.

The historical climatic stability of the Appalachian Mountains is likely the reason this region is a biodiversity hotspot for many clades including Plecoptera (Sheldon, 2012); however, projected warming will likely shift species' climatic niches in this region (Milanovich and others, 2010); some montane species will be unable to track niche shifts. High elevation species, like many Plecoptera spp., are unable to shift ranges and are particularly vulnerable to warming temperatures, creating summit traps. Additionally, the poor

dispersal ability of many Plecoptera spp. make them unlikely to follow suitable climate if shifts happen across large distances and involve movement through inhospitable habitat.

The three Appalachian stonefly species Remenus kirchneri, Acroneuria kosztarabi, and Tallaperla lobata have different geographic and elevational ranges and differing risk from climate-change-induced shifts in suitable habitat. A. kosztarabi with its wide geographic (fig. 1A) and elevational distribution (184-944 m; Verdone and Kondratieff, 2018) is unlikely to experience large declines in distribution because of range shifts and is not at risk from summit traps. In comparison, R. kirchneri has a smaller geographic distribution

(fig. 1A) and is only found above 395 m in elevation (Verdone and Kondratieff, 2018). Although R. kirchneri may lose habitat at the warm, low elevation edge of its distribution with future warming, given its broad elevational distribution, suitable habitat is likely to be retained at higher elevations. Finally, T. lobata is most at risk from shifts in suitable habitat. This species has a very narrow geographic distribution (fig. 1A) and only occurs above 592 m in elevation (Verdone and Kondratieff, 2018) with most documented occurrence points above 800 m in elevation (fig. 1C). Tallaperla lobata is at risk from summit traps caused by warming temperatures.

Table 9. Direct and indirect potential effects of climate change on Remenus kirchneri, Acroneuria kosztarabi, and Tallaperla lobata.

Effect	Climate factor	Direct mechanisms	Indirect mechanisms	Citations
Distribution shift	Increasing temperature Changing precipitation	Narrow thermal tolerance	Changing landcover	Hotaling and others (2020); Sweeney and others (1986); Hogg and Williams (1996); Shah and others (2014); and Sheldon (2012).
Physiological stress	Increasing temperature Changes in precipitation Decreased runoff Secondary effects • Stream temperature • Flow rate o Dissolved oxygen content o Contaminant loads	Metabolic rate increase Emergence/adult size decrease	Changing landcover Decreasing food access • Leaf litter availability • Leaf litter access • Decreased detritovore populations	Birrell and others (2020); Durance and Ormerod (2009); Jacobsen (2020); Anderson and Cummins (1979); Piano and others (2020); and Buzby and Perry (2000).
Reduced reproductive success	Increasing temperature Changes in precipitation Decreased runoff	Decreased hatching success Low adult size • Decreased fecundity • Decreased oviposition site selection Buffered by changes in breeding and emergence phenology	Changing landcover Decreasing food access • Leaf litter availability • Leaf litter access Decreased detritovore populations	Nebeker (1971); Collier and Smith (2000); Brittain (1990); Hogg and Williams (1996); Taylor and others (1998); Carey and others (2021); Cheney and others (2019); and Grubbs and others (2006).
Reduced survival	Increasing temperature Heavy rainfall events Decreased runoff	Changes in flow intermittency Buffered by emergence plasticity	Increased contaminant loads	Piano and others (2020); McRoberts and Grubbs (2021); and DeWalt and Ower (2019).

Physiological Stress

Increased Stream Temperatures Will Likely Thermally Stress Plecoptera Species

Restricted distributions in Plecoptera spp. likely relate to the interacting effects of stream temperature and oxygen availability on multiple physiological processes. Where studied, Plecoptera species (even alpine specialists) have higher critical thermal maximum than expected based on experienced stream temperatures (Hotaling and others, 2020). High stream temperatures are unlikely to be directly lethal to larvae. Rather, increased temperature, especially for longer periods, decreases hatching rates and depletes larval energy availability (Hotaling and others, 2020). The effects of the larval environment have implications for the fitness and longevity of adults (Nebeker, 1971).

Energy demand increases with temperature (Birrell and others, 2020). At higher stream temperatures, larvae require more energy; absent additional energy inputs, they may be smaller in size. Increasing metabolic rates also increases oxygen demand; however, dissolved oxygen availability is likely to decrease with warmer temperatures and decreased streamflow conditions (Daufresne and others, 2007; Durance and Ormerod, 2009; Jacobsen, 2020). Increasing energy and oxygen requirements with decreasing oxygen availability in warming streams will likely lead to tradeoffs among growth, reproduction, and locomotor movement, resulting in reduced adult fitness and dispersal ability (see the "Reproduction" section).

Within our study domain, air temperatures are increasing especially in the summer. Combined with potentially decreasing runoff, stream temperatures are likely to increase, and dissolved oxygen is likely to decrease with higher diurnal variability. Though there are no species-specific physiological studies on the three Appalachian stoneflies *Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata*, thermal stress on physiological processes from increasing stream temperatures is likely to be comparable to other stonefly species. Species like *A. kosztarabi* that inhabit a large latitudinal and elevational gradient may have broader thermal reaction curves for physiological processes, increasing their adaptive capacity.

Phenology

Plecoptera Breeding Phenology is Affected by Streamflow and Stream Temperature

Some Plecoptera spp. seem to have adapted to adjust breeding onset based on the timing of seasonal conditions. In Australia, the stonefly *Leptoperla australica* altered its breeding phenology from autumn to winter to account for altered streamflow (Carey and others, 2021). Many Plecoptera spp. demonstrate plasticity in life history timing. Altering breeding onset often requires increased time as adults to avoid warm water and low flow. Warming temperatures

are expected to decrease adult longevity in Plecoptera spp. (Collier and Smith, 2000), making it unlikely that many species will be able to substantially alter breeding phenology. The three Appalachian stonefly species *Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata* have a brief adult life stage that may be further reduced by increasing stream temperatures during larval development. Whether these species have the adaptive capacity to adjust breeding phenology is unclear. Changes in breeding phenology are commonly observed in intermittent stream systems; these three species use permanent stream habitats, which are unlikely to switch to intermittent in the future.

Plecoptera Emergence Timing Dependent on Temperature and Streamflow

Increasing stream temperature decreases the length of larval development leading to earlier emergence (Cheney and others, 2019). In addition to stream temperature, stream drying can also affect emergence timing for those species adapted to intermittent stream conditions (Grubbs and others, 2006). Plasticity in the timing of emergence may buffer some stonefly species from changes in stream conditions related to climate; however, many of these adaptive traits are only present in species from historically intermittent habitats (McRoberts and Grubbs, 2021).

For the three Appalachian stonefly species *Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata*, stream temperatures are likely to increase and there may be instances of decreased flow, though the change to intermittent flow is unlikely. Species with longer life cycles like *A. kosztarabi* and *T. lobata* will be less buffered by plasticity in phenology. Larvae of these species are in the stream for more than 1 year, and only the cohort at the end of their larval period would be able to avoid low water through early metamorphosis.

Survival

Changing Stream Permanence May Reduce Larval Survival in Plecoptera species with Longer Life Cycles

Changes from perennial to intermittent flow or changes in the timing and duration of intermittent flow has the greatest effect on Plecoptera spp. that have a life cycle longer than 1 year (Piano and others, 2020). Univoltine species may have the ability to develop quickly and emerge before water levels are low (McRoberts and Grubbs, 2021); other life history strategies that confer advantages to changing flow duration include dormant egg or larval stages capable of surviving dry periods (Bogan, 2017). Stream intermittency acts as an environmental filter; many Plecoptera spp. lack the adaptive capacity to survive in these environments. Perennial streams

accommodating species with and without adaptations for intermittent flows tend to have higher diversity of Plecoptera spp. (McRoberts and Grubbs, 2021; Smith and others, 2003).

Climate change may alter streamflow duration in multiple ways. Perennial streams could change to intermittent and vice versa; intermittent streams could change in the timing and duration of no flow (Eng and others, 2016). These changes would affect the Plecoptera community, changing the richness and abundance of Plecoptera spp. in a stream system. Even rare dry events are likely to have profound effects on communities. Because of the limited dispersal ability of many Plecoptera spp., drying events have long lasting effects. Recolonization rate depends on the dispersal ability of the species and the geographic spread of a drying event (Datry and others, 2011).

Changes to streamflow duration and timing will be important climate effects for many Plecoptera spp.; however, within the domain of this study, changes to streamflow are likely to have less of an effect because of stream type and species adaptive capacity. The three Appalachian stoneflies Remenus kirchneri, Acroneuria kosztarabi, and Tallaperla lobata occupy streams that are primarily classified as perennial and stable though prone to seasonal extremes. Future projected reductions in annual and summer runoff may increase the probability of low water events in Appalachian stonefly streams, but streams are unlikely to become intermittent. Species-specific traits increase the adaptive capacity of these species to withstand the effects of occasional low water events. A. kosztarabi has a life cycle greater than 1 year, but mainly occupies midsized streams (Verdone and Kondratieff, 2018), which are less likely to experience zero flow. Tallaperla lobata also has a life cycle that appears to be longer than 1 year; however, T. lobata may have similar adaptive capacity to other closely related species (Verdone and Kondratieff, 2018) that use cohort splitting, with some eggs going through diapause during drier months which buffers the population from low flow and high temperature (Schultheis and others, 2002). Finally, R. kirchneri has a univoltine life cycle with emergence beginning in May (Verdone and Kondratieff, 2018), which may allow this species to emerge before low water periods.

Reproduction

Reproductive Success Decreases Outside of Optimal Thermal Conditions

Adult longevity and fitness in Plecoptera spp. reflect larval conditions related to water temperature and food supply (Nebeker, 1971). In warmer streams, stoneflies develop faster at the expense of size at emergence, leading to smaller adults (Brittain, 1990; Hogg and Williams, 1996). Fecundity, primarily the number of ova produced, is related to size at metamorphosis for Plecoptera spp., with smaller individuals producing fewer ova (Hogg and Williams, 1996; Taylor and others, 1998). Lower adult body size also means less energy

stored from the larval stage (the primary time in the life cycle when Plecoptera eat), which can reduce flight activity and limit dispersal in adults (Larsen and others, 2016). Adult Plecoptera with decreased energy stores may be unable to find suitable oviposition sites. These effects are compounded by reduced locomotor ability in air temperatures outside of suitable range (Collier and Smith, 2000).

Plecoptera hatching success is dependent on stream temperature, decreasing sharply after a certain temperature threshold (Brittain, 1990). The optimal temperature range for hatching varies by species, but for most Plecoptera spp., hatching success is highest from 10 to 15 °C. Many species can have high hatching success even at temperatures as low as 5 °C, but most drop off in success beyond 15 °C (Brittain, 1990).

Stream temperatures in the distributions of the three Appalachian stoneflies *Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata* are likely to increase. For narrowly distributed *T. lobata* and *R. kirchneri*, it is likely that current stream temperatures align with optimal hatchling success and adult fecundity. Increasing stream temperatures may lower reproductive success in both species, though species-specific data are not available. *T. lobata* is present only in forested streams, and most localities for *A. kosztarabi* and *R. kirchneri* are highly forested (Verdone and Kondratieff, 2018), which may buffer streams from some future warming (Trimmel and others, 2018).

Habitat

Increased Contaminant Loads May Decrease Stream Habitat Suitability

Plecoptera diversity is commonly used as a metric to assess water quality because species in this order are assumed to be sensitive to freshwater pollutants (Pond, 2012). Plecoptera spp. are often the first insects lost in streams after nutrient enrichment or other habitat degradation (DeWalt and Ower, 2019). One potential mechanism for Plecoptera sensitivity to nutrient enrichment is through algal growth, especially in agricultural areas (U.S. Environmental Protection Agency [EPA], 2008). Algal growth may inhibit access to leaf litter for shredding species and access to holds on substrates for larval Plecoptera causing drift.

Increasing precipitation, especially heavy rainfall events in areas with impervious surface or agriculture, may wash more contaminants into streams (EPA, 2008). Additionally, increasing variability in precipitation timing may lead to more frequent or pronounced dry events, which can increase concentrations of contaminants in water. The three Appalachian stoneflies *Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata* may experience increased frequency of heavy rainfall events but overall reduction in runoff. These combined climate changes may lead to more contaminants during heavy rainfall pulses and higher concentration of contaminants from decreased streamflow.

Climate Driven Changes in Tree Cover and Composition May Exacerbate Other Stressors

Tree species have ecological requirements commonly associated with specific temperature and precipitation regimes. Like stoneflies, climate change is likely to cause suitable areas for tree species to shift in latitude and elevation. Other climaterelated disturbances like forest fires and landslides are also likely to increasingly affect tree canopy cover and community structure (Peterson and Reich, 2007). Slow growing tree species with low recruitment are likely to be particularly vulnerable to increasing disturbances. In the Appalachians, fire risk is likely to increase under high emissions scenarios, though to a lesser extent compared to surrounding areas (Gao and others, 2021).

Butler and others (2015) found that for the Central Appalachians (not shown) (the northern edge of our study domain), climate change will likely reduce suitable habitat for tree species that are at the southern edge of their climate suitability and (or) have low adaptive capacity like *Fraxinus nigra* (Marsh) (black ash). Other tree species currently at the northern edge of their range in the Central Appalachians and (or) with high adaptive capacity like *Quercus marilandica* (Münchh) (blackjack oak) may increase. The likelihood of tree species in our study area declining or increasing will depend on whether they are at the edge of their range and their adaptive capacity.

Changing forest composition would affect food availability for Plecoptera shredder species, which rely on decomposing leaves. Type, quantity, and quality of leaf litter can affect life history for stream invertebrates like Plecoptera spp. (Anderson and Cummins, 1979), though trophic ecology for most Plecoptera spp. is still poorly understood (Tierno de Figueroa and López-Rodríguez, 2019). Additionally, changing tree cover could affect the shading of streams, which currently buffers some of the effects of air temperature increases on stream warming. Predicting how forest cover and composition will change with climate and alter stream temperatures and litter availability in the habitats of *Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata* requires further study.

Biotic Interactions

Reduced Flow May Decrease Shredder Species' Access to Food Resources

Flow reductions can affect shredder Plecoptera spp. (like *Tallaperla lobata*) food acquisition in multiple ways. Less organic matter like leaves may wash into and through the stream systems (Piano and others, 2020). Reduced flow can allow fine sediment deposits to form, preventing access to leaf litter (Piano and others, 2020). Additionally, increasing atmospheric carbon dioxide may reduce the nutritional quality of leaf litter for detritivorous shredders (Tuchman and others, 2002), further decreasing energy assimilation in addition to changes from increased stream temperature and decreased dissolved oxygen content (see the "Physiological Stress"

section). Changes to detritovore populations' density and size could have cascading effects on other parts of the food web including predatory stoneflies like *Remenus kirchneri* and *Acroneuria kosztarabi* (EPA, 2008).

Increased Stream Temperatures May Decrease Food Resource Availability

Changes in temperature, precipitation, and flow rates affect leaf litter deposition and decomposition rates. Buzby and Perry (2000) modeled the shredder population, including stoneflies, and found that invertebrate processing increased in moderately wet years. In years with too much rainfall, leaf material was transported downstream before being consumed. Higher temperatures may also increase the processing rate of leaf pack early in the year; however, this can lead to less availability of leaf pack for food in the summer. A meta-analysis on litter decomposition studies from 1993 to 2017 found that elevated temperatures significantly increased decomposition rates by microbes and invertebrates regardless of region or litter composition (Amani and others, 2019).

Conclusion

Increasing annual and summer temperatures will likely affect multiple processes in the life cycles of *Remenus kirchneri*, *Acroneuria kosztarabi*, and *Tallaperla lobata*. Despite the lack of identified critical thresholds for these focal species, there is strong evidence that increased temperatures lead to increased metabolic rate and decreased reproductive success in Plecoptera spp. Within the distributions of these three species, there is high confidence that annual and summer mean temperatures will increase through the 21st century. Further experimental and observational research identifying optimal temperatures, physiological thresholds, and temperature dependent cues for emergence and reproduction is necessary to quantify the effects of thermal stress on these and other Plecoptera spp.

Most Plecoptera spp. rely on clean, fast-moving freshwater and are likely sensitive to direct changes in the hydroclimate and indirect changes to the aquatic habitat. The direction of future changes in runoff and precipitation is highly variable in the eastern United States. Future conditions may be wetter or drier compared to current and historical records; the full range of projections presented here should be used as a guide for the range in future conditions. Additionally, without established species-specific sensitivities to flow, sedimentation, and contaminant loads, it is difficult to directly quantify how climate change will affect physiology and vital rates in specific Plecoptera spp. Increased monitoring of Plecoptera larvae under current aquatic habitat conditions will be necessary to establish connections among the aquatic habitat and species presence and reproductive success. Similarly, increased sampling of presently occupied localities combined with frequent resampling will be critical for documenting elevational and latitudinal shifts in Plecoptera spp. distributions.

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