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Projected warming portends seasonal shifts of stream temperatures in the Crown of the Continent Ecosystem, USA and Canada

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Abstract Climate warming is expected to increase stream temperatures in mountainous regions of western North America, yet the degree to which future climate change may influence seasonal patterns of stream temperature is uncertain. In this study, a spatially explicit statistical model framework was integrated with empirical stream temperature data (approximately four million bi-hourly recordings) and high-resolution climate and land surface data to estimate monthly stream temperatures and potential change under future climate scenarios in the Crown of the Continent Ecosystem, USA and Canada (72,000 km²). Moderate and extreme warming scenarios forecast increasing stream temperatures during spring, summer, and fall, with the largest increases predicted during summer (July, August, and September). Additionally, thermal regimes characteristic of current August temperatures, the warmest month of the year, may be exceeded during July and September, suggesting an earlier onset

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and extended duration of warm summer stream temperatures. Models estimate that the largest magnitude of temperature warming relative to current conditions may be observed during the shoulder months of winter (April and November). Summer stream temperature warming is likely to be most pronounced in glacial-fed streams where models predict the largest magnitude (> 50%) of change due to the loss of alpine glaciers. We provide the first broad-scale analysis of seasonal climate effects on spatiotemporal patterns of stream temperature in the Crown of the Continent Ecosystem for better understanding climate change impacts on freshwater habitats and guiding conservation and climate adaptation strategies.

1 Introduction

Stream temperature is a fundamental driver of abiotic and biotic processes within freshwater ecosystems (Kelleher et al. 2011). Climatic changes associated with atmospheric warming are causing increases in temperatures within many streams and rivers worldwide, altering physical, chemical, and biological processes in aquatic ecosystems (Shelton 2009). Increasing water temperatures caused by climate warming can impact abiotic characteristics of freshwater systems by decreasing oxygen levels, increasing toxicity and pH levels, and modifying biogeochemical processes (Poff et al. 2002). Additionally, thermal variations due to climate warming can impact biotic components of aquatic ecosystems, such as aquatic metabolism (i.e., photosynthesis rates), and the physiology, survival, abundance, distribution, and phenology of aquatic organisms (Schindler 2001). An important component of understanding climate impacts on freshwater systems, therefore, will be simulating climate-induced change across spatial and temporal domains, so that ecosystem response can be better understood.

Over the past century, the northern Rocky Mountains have warmed two to three times the rate of the global average, causing seasonal shifts in temperature and precipitation patterns (Pederson et al. 2010). Winter and spring warming and declining snowpack have resulted in an earlier onset of spring snowmelt (~ 2–3 weeks) and declining baseflows during the summer and fall months (Rood et al. 2008). Climate records indicate an earlier onset and later extension of the summer season, with extremely hot days (> 32 °C) occurring 24 days earlier and lasting 14 days longer than early twentieth century (Pederson et al. 2010). Stream temperatures are also rising and have been linked to long-term increases in air temperatures and associated changes in the hydrological cycle (Isaak et al. 2012). Consequently, trend analyses of stream temperature records in the Pacific Northwest show increases in the magnitude and duration of warm summer temperatures, with estimated increases up to 0.22 °C/decade (1980–2009; Isaak et al. 2012) and warmer temperatures beginning a full month earlier and persisting 2–3 weeks later (1950–2006; Crozier et al. 2008). Climate model simulations forecast that these mountainous systems will likely continue to trend toward an earlier onset of spring runoff (MacDonald et al. 2011; Rood et al. 2008), warmer drier summers (Westerling et al. 2007), reduced summer flows, increased late summer drought (Pederson et al. 2010), and warmer summer stream temperatures (Jones et al. 2014; Isaak et al. 2015). Despite future forecasts of climate warming impacts on summer stream temperatures, changes in seasonal thermal distributions of stream systems and linkages with future climate change have not been assessed across the Crown of the Continent Ecosystem (CCE), USA and Canada.

Stream temperature models can be used to evaluate underlying physical processes affecting thermal dynamics in freshwater ecosystems and predict thermal distributions across space and time continuums (Webb et al. 2008). Physically based models are useful for quantifying total

energy fluxes occurring at both the air-water and streambed-water interfaces, but require significant amount of data inputs (e.g., meteorological data, stream geometry, land cover classifications, riparian shading, soil moisture indices, hydrology). Therefore, physically based models are generally applied across small spatial domains, at coarse resolutions, or at individual site locations (MacDonald et al. 2014; Wu et al. 2012). Spatial statistical stream temperature models are frequently used to simulate thermal changes in freshwater ecosystems and are effective for describing landscape-scale patterns of climate-induced temperature change and potential impacts on ectothermic organisms. Common applications of such landscape-scale models include stream temperature estimation during the warmest month of the year (e.g., August), when aquatic species are assumed to be most thermally sensitive (Isaak et al. 2011; Jones et al. 2014). Generally, these models are employed in a “climate envelope” type approach, where summer temperatures are used to define climatic conditions (i.e., thermal niches) under which species are likely to occur, and future distributions are forecasted by extending these relationships to future climate scenarios. Such temporally constrained models, however, are limited to spatial pattern analysis for understanding potential climate impacts on aquatic species and critical habitats. Creating frameworks that link seasonal climate patterns with stream temperature variations to forecast spatiotemporal changes in thermal distributions at the landscape scale is needed to strengthen our understanding of potential impacts to aquatic species (i.e., spatial distributions, phenology, and connectivity) and provide an integral resource for guiding landscape-scale conservation and climate adaptation strategies.

Here, we compiled a comprehensive database of stream temperature records and high-resolution climate data to predict current and future stream temperatures across the CCE - one of the most ecologically diverse ecosystems in the Rocky Mountains of North America. This transboundary ecosystem is considered a regional and range-wide stronghold for many native aquatic species (Hauer and Muhlfeld 2010) and spans several management jurisdictions in Montana, USA, and Alberta and British Columbia, Canada. As tools for collaborative landscape conservation and climate adaptation planning are critically needed, we provide the first broad-scale analysis of spatiotemporal patterns of stream temperature change in the CCE. Specifically, we used spatially explicit statistical stream temperature models to forecast mean monthly stream temperatures under current and future climate scenarios. Simulated model results were then used to assess the magnitude and variation of predicted change across time (i.e., months) and space. The model framework described within provides a relatively simple approach to characterizing stream temperatures and analyzing broad spatiotemporal patterns of climate-induced change across large landscape domains.

2 Data and methodology

2.1 Study area and stream temperature data

The CCE (72,000 km²) is considered the hydrologic apex of North America and source for three major continental river drainages, the Columbia, Missouri, and Saskatchewan, that flow to the Pacific, Atlantic, and Arctic oceans, respectively. The CCE is bounded by the Rocky Mountain Trench on the west and the prairie foothills on the east, while the interior consists of a complex topographic landscape shaped from belt series mountain ranges, with elevational gradients ranging from 740 to 3338 m. As a result, the region consists of headwater streams

that originate in high alpine environments, subalpine streams that flow through forested watersheds, and low-elevation or valley bottom streams, which are generally characterized by alluvial floodplains. The ecosystem is composed of watersheds in various stages of deglaciation—large valleys where glaciers retreated 15,000 years ago and high-elevation valleys where glaciers are still retreating today (Pederson et al. 2007). Climate is driven by a unique convergence of climate zones along the narrowest point along the Rocky Mountain cordillera. Pacific Northwest Maritime weather patterns control the climate west of the Continental Divide and continental air masses (e.g., northern boreal Arctic and eastern Great Plains) moving from the north and south drive climate patterns east of the divide (Hauer et al. 2007).

We assembled an extensive stream temperature database consisting of approximately four million bi-hourly measurements recorded at 743 sites ($N_{\text{summer}} = 720$; $N_{\text{fall}} = 297$; $N_{\text{spring}} = 407$) during the years of 1990–2013 (Online Resources 1 and 2). Monitoring sites ranged from mainstem rivers to forested headwater and alpine streams, including glacial and lake systems. Stream temperatures were recorded with digital thermographs (Hobo and Tidbit models; Onset Computer Corporation, Pocasset, Massachusetts, USA; accuracy ± 0.2 °C) at bi-hourly or hourly intervals using standard methodology (Dunham et al. 2005; Isaak et al. 2013). Of the total number of unique sites, 423 sites were part of long-term monitoring efforts conducted by the US Geological Survey. Data from the remaining 319 sites were synthesized from natural resource agencies across Montana, British Columbia, and Alberta (including US Fish and Wildlife; Montana Fish, Wildlife, & Parks; National Park Service; US Forest Service; Swan Ecosystem Center; Environmental Protection Agency; Parks Canada; Alberta Environment and Parks; and BC Ministry of Environment). Temperature measurements were then summarized to mean monthly temperatures for each site and year of the study period and used in the parameterization of seasonal models.

2.2 Model drivers and hydrography

First-order processes influencing thermal heterogeneity of freshwater ecosystems begin at the largest spatial scale and include regional and seasonal climate patterns (i.e., temperature and precipitation; Kelleher et al. 2011). Because air temperature has strong direct (i.e., sensible heat transfer and long-wave atmospheric radiation) and indirect effects (i.e., hydrologic patterns, climate warming) on stream temperatures, it is commonly used in statistical stream temperature prediction as a surrogate for net radiation exchange (Webb et al. 2008). Mean monthly Daymet air temperature raster surfaces (1 km resolution; Thornton et al. 2012) were temporally joined to site-specific temperature records and used as the principle climate driver in the stream temperature models. This statistical approach relies on the correlative and linear nature of the air-water temperature relationship to predict climate-induced stream temperature change (Benyahya et al. 2007). Because this relationship fails to remain linear at the lower bounds of the air temperature range, near or below 0 °C (e.g., when air temperatures are below the freezing limit; Letcher et al. 2016), the winter season was excluded from subsequent analyses. Prior to model development, mean monthly air-water temperature correlations were evaluated for each seasonal model.

Topography can cause climate patterns to deviate from regional trends influencing temperature gradients, watershed structure, and function (Jones et al. 2017; Loarie et al. 2009). We used topographic predictor variables (elevation, slope, and aspect) to represent second-order effects (i.e., watershed scale) accounting for geomorphic features influencing stream temperature.

Digital elevation models (DEMs) from the National Hydrography Data Plus (USGS) dataset in the USA (30 m) and GeoBase in Canada (20 m) were mosaicked together and resampled to a 30-m resolution using ArcGIS version 10.2 (Environmental Systems Research Institute, Redlands, CA, USA). Slope and aspect (30 m) surfaces were derived from the final DEM product.

Third-order effects included the presence of lakes and glaciers at the stream reach scale. We created categorical predictor variables, *lake* and *glacier*, to investigate downstream thermal influences of lakes and glaciers on sites in our study (Giersch et al. 2015; Melinna et al. 2002). Based on empirical data used in the model, we created a lake size threshold for the warming effect, where the smallest lake within our study was used to designate the lower lake size threshold. Because model simulations predict that most glaciers in the CCE will disappear by 2030 (Hall and Fagre 2003), our model simulations included a null glacier effect for all future climate scenarios. To interpolate stream temperatures across the network, stream segments downstream of lakes and glaciers were considered thermally affected and were digitized as such to the confluence of the next highest stream order. A *month* effect was also included to account for intermonthly variations within each seasonal model.

Due to the transboundary nature of the CCE, a stream network was developed by merging USGS National Hydrographic Datasets (NHD) with NHD harmonized datasets for the USA-Canada transboundary watersheds and National Hydro Network datasets for the remaining watersheds in Alberta and British Columbia (NRC 2007; USGS 2013). All covariates were attributed to stream temperature records at the individual locations for model parameterization and then to the stream network (100 m resolution) for model interpolations.

2.3 Spatial statistical models and climate change analysis

Because temperature variation is driven by seasonal processes and patterns, seasonal temperature models were used to predict monthly stream temperatures across the CCE. Correlations within and among mean monthly stream temperature observations (n) were used to partition seasonal models: spring (April, May, and June: $n = 1716$), summer (July, August, and September: $n = 2301$), and fall (October and November: $n = 1150$; Online Resources 2 and 3). A spatial hierarchical model framework (e.g., mixed effect generalized linear regression model) was used to parameterize seasonal temperature models (SAS version 9.4; Jones et al. 2014). Watershed divisions (Hydrologic Unit Code 4) were treated as a random effect to account for spatial autocorrelation among sample sites within each watershed. Moran's I test statistic was calculated for model residuals to test that spatial autocorrelation was explained in each of the seasonal models (Legendre and Legendre 1998). The Akaike information criterion (AIC) was used to subset the best set of fixed effects across all models, while forward and stepwise elimination methods were used to remove insignificant parameters, resulting in the best predictive model with fewest covariates. We used cross-validation to compare the predictive accuracy of each model, where data was split into training and validation sets composed of equal percentages (10%) of sites randomly sampled from each watershed (Hydrologic Unit Code 4). Root mean square error (RMSE) of model predictions and Pearson correlation coefficients (r) between predicted and observed values were used to assess predictive accuracy of each model iteration. Prior to model interpolations, each model was refit to the pooled set of observations from the training and validation sets.

Coupled models from the Canadian Center for Climate Modeling and Analysis and the Intercomparison Project 5 (CMIP5) were used as the basis for the future climate projection analysis, where the Canadian Regional Climate Model 4 (CanRCM4) is nested within the

second-generation Canadian Earth System Model 2 (CanESM2). The CanRCM4 downscaling improves annual responses of precipitation, evapotranspiration, moisture flux convergence, and terrestrial water storage estimates and biases, providing more realistic estimates of large-scale climatic flow patterns of the coarser resolution CanESM2 (Caya and Laprise 1999). Two representative concentration pathway (RCP) scenarios, RCP 4.5 and RCP 8.5, from the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC 2013) were chosen to describe future climate warming. The RCP scenarios are based on the peak or stabilization value of the radiative forcing by 2100. These scenarios span a range of greenhouse gas emission scenarios between moderate (RCP 4.5) and extreme scenarios (RCP 8.5). The RCP 4.5 scenario accounts for stabilization at 4.5 W m^{-2} around 2100, while the RCP 8.5 scenario implies a radiative forcing of 8.5 W m^{-2} by 2100 and further rising beyond this point. Simulating stream temperatures based on future climatic changes relies on predictive models that estimate baseline conditions from which future changes can be assessed (Elliott and Elliott 2010). For the baseline model simulations, mean monthly air temperature surfaces (Daymet) were summarized for the period (1986–2005) and used in the seasonal models to predict average monthly temperatures. At landscape scales, global temperature anomalies, whether above or below historic averages, are reflected in thermal distributions of freshwater ecosystems (Isaak et al. 2012). To evaluate model capacity in capturing year to year variability within the baseline period, stream temperature predictions were created for a colder than average year (1993) and a warmer than average year (2003). Climate records indicate that 1993 was the last year that daily average lows outnumbered daily record highs, while 2003 was one of the top 10 warmest years on record (NOAA 2015; Pederson et al. 2010). To predict future conditions, gridded monthly air temperature changes (Online Resource 4) from the RCP 4.5 and 8.5 scenarios (1 km resolution) were summarized for the near-future 2026–2045 (2035) and mid-future periods 2066–2085 (2075). These surfaces were then added to the baseline surfaces and used in a delta-change approach to assess future air temperature warming effects on stream temperatures.

To estimate the magnitude of stream temperature change predicted from the climate warming simulations, we calculated mean absolute and relative change (i.e., percent change) from the baseline to future periods and examined regional shifts in the onset and duration of seasonal temperatures based on current temperature regimes. Additionally, thermal maps of absolute change were generated to describe spatial and temporal variation across the ecosystem. Variability (i.e., dispersion) of model predictions was evaluated by calculating the coefficient of variation (CV), while Kolmogorov-Smirnov non-parametric tests were used to examine statistical significance of change in thermal distributions (i.e., empirical distribution functions) between the baseline and future scenarios.

3 Results

3.1 Stream temperature models

Monthly air-water temperature correlations showed a strong linear relationship at the monthly time step and landscape scale ($r_{\text{spring}} = 0.78$, $r_{\text{summer}} = 0.68$, $r_{\text{fall}} = 0.79$). Seasonal models were parameterized with *air temperature*, *elevation*, *slope*, *lake*, *glacier*, and *month* covariates. All predictors were statistically significant ($p < 0.05$) and parameter signs in agreement with their expected influence across seasons (Online Resource 3). We chose seasonal models that performed

best with the validation data (*spring*: $r = 0.90$ and $\text{RMSE} = 1.31$ °C, *summer*: $r = 0.90$ and $\text{RMSE} = 1.38$ °C, *fall*: $r = 0.86$ and $\text{RMSE} = 1.06$ °C) and retained good predictive ability with the training data (*spring*: $r = 0.91$ and $\text{RMSE} = 1.17$ °C, *summer*: $r = 0.90$ and $\text{RMSE} = 1.23$ °C, *fall*: $r = 0.90$ and $\text{RMSE} = 0.91$ °C; Online Resource 3). The covariate *aspect* did not improve predictive ability in the seasonal models and was the only parameter removed in the model selection process. Random effects were statistically significant ($p_{\text{spring}} = 0.02$, $p_{\text{summer}} = 0.01$, $p_{\text{fall}} = 0.03$), and Moran's I showed that spatial autocorrelation was adequately explained in the models ($I_{\text{spring}} = 0.002$, $I_{\text{summer}} = 0.0008$, $I_{\text{fall}} = 0.0006$). A significant warming effect of stream temperature was observed for all sites downstream of lakes ($p < 0.0001$); this effect was estimated at + 3.05 °C during the summer season, + 1.53 °C during the fall season, and + 0.83 °C during the spring season. Conversely, a significant cooling effect was observed for sites downstream of glaciers ($p < 0.0001$). This effect was estimated as a - 2.15 °C cooling effect during the summer season, - 0.79 °C during the fall season, and - 1.61 °C during the spring season. Parameter signs also suggest that higher gradient streams may be slightly cooler during the summer months and warmer during the spring and fall months. The model clearly captured year to year variability in thermal conditions for 2 years representing global anomalies in historic air temperatures (Fig. 1); average stream temperature for 1993 was 8.7 °C, and average temperature in 2003 was 11.9 °C. A scatter plot of the predicted and observed values for sites corresponding to the years in Fig. 1 (1993 and 2003) illustrates model accuracy and strong linear correlations between observed and predicted values (Online Resource 5).

3.2 Predicted stream temperature change

Projections under moderate and extreme climate change scenarios forecast that the largest increases in stream temperatures will occur during the summer months (July, August, and September). While predicted temperature increases for the RCP 4.5 and 8.5 scenarios were

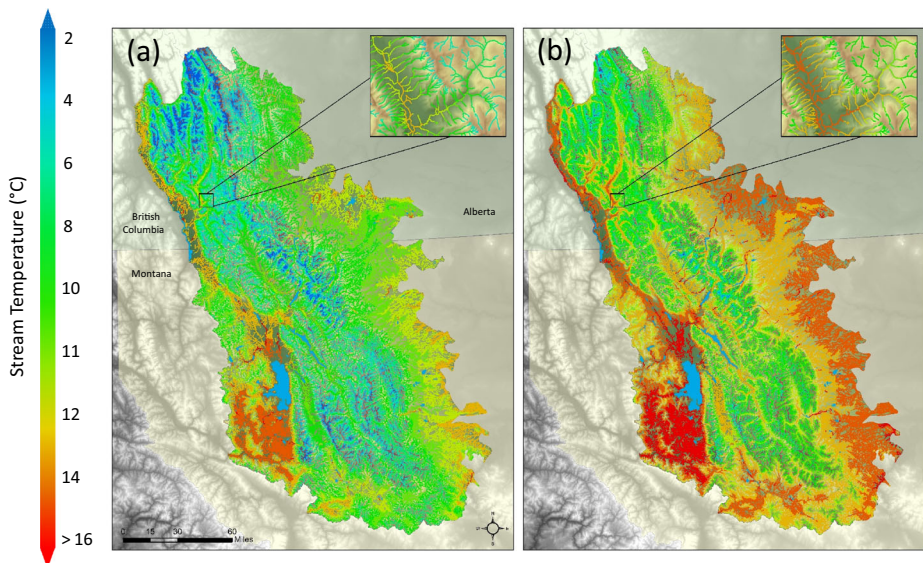


Fig. 1 Average August stream temperatures (°C) are shown for 1993 (a), a colder than average year, and 2003 (b), one of the top 10 warmest years on record

similar in magnitude for 2035, predicted increases under the RCP 8.5 scenario were about 40–100% greater than the RCP 4.5 scenario for 2075 (Online Resource 6). Thermal distributions show that for all future climate simulations, mean July stream temperatures are predicted to exceed baseline August conditions (Fig. 2). Similarly, September stream temperatures are predicted to approximate baseline August temperatures for all future climate scenarios except RCP 8.5 (2075) where temperatures are anticipated to far exceed baseline August temperatures (Fig. 2). Relative change statistics show notable increases for the shoulder months of winter (i.e., April and November), while relative changes are considerably lower for May and October (Online Resource 6). Although calculations of CV reveal high variability in model predictions for spring, particularly April, variability for the summer and fall months is comparably low (Online Resource 6). Kolmogorov-Smirnov tests for significant change (i.e., warming) between the baseline and future scenarios were statistically significant ($p < 0.0001$), indicating significant differences in the empirical distributions of temperatures.

Spring model simulations show that spatial warming patterns for April and May vary longitudinally, increasing from east to west, whereas warming patterns for June are strongest in the southern and central portions of the ecosystem (Fig. 3; Online Resource 7). Warming patterns for the summer months are most prominent in the central portion of the ecosystem, which consists of montane watersheds and higher elevation streams (Fig. 4; Online Resource 8). In addition, with the complete loss of glacial masses, glacial-fed streams may observe warming rates 50% larger in magnitude than non-glaciated streams. Fall patterns are highly variable minus a clear pattern in the mid-future November simulations which shows increased warming in the western extents with maximum warming occurring in the lower elevation streams around Flathead Lake in Montana (Fig. 5; Online Resource 9).

4 Discussion and summary

4.1 Climate effects on seasonal stream temperature distributions

For mountain ecosystems such as the Crown of the Continent, atmospheric warming has resulted in temporal shifts in seasonal windows, including a later onset of fall and winter and

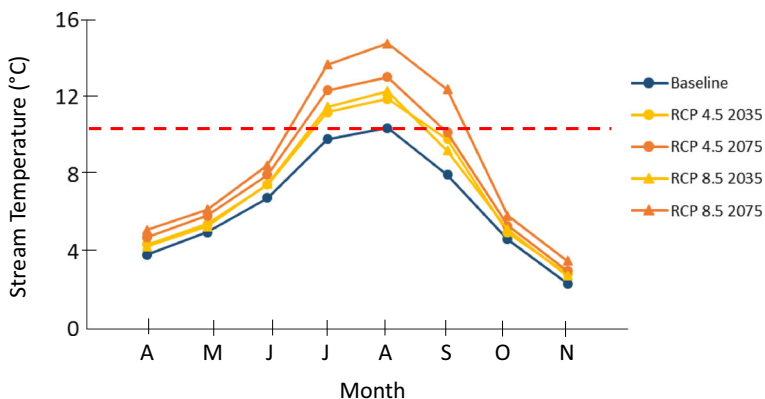


Fig. 2 Mean monthly stream temperatures under baseline (1986–2005) and future climate scenarios. Warmest temperature regimes under baseline simulations (August) are emphasized with red dotted line. See Online Resource 6 for details including mean stream temperatures, predicted change, and coefficient of variation

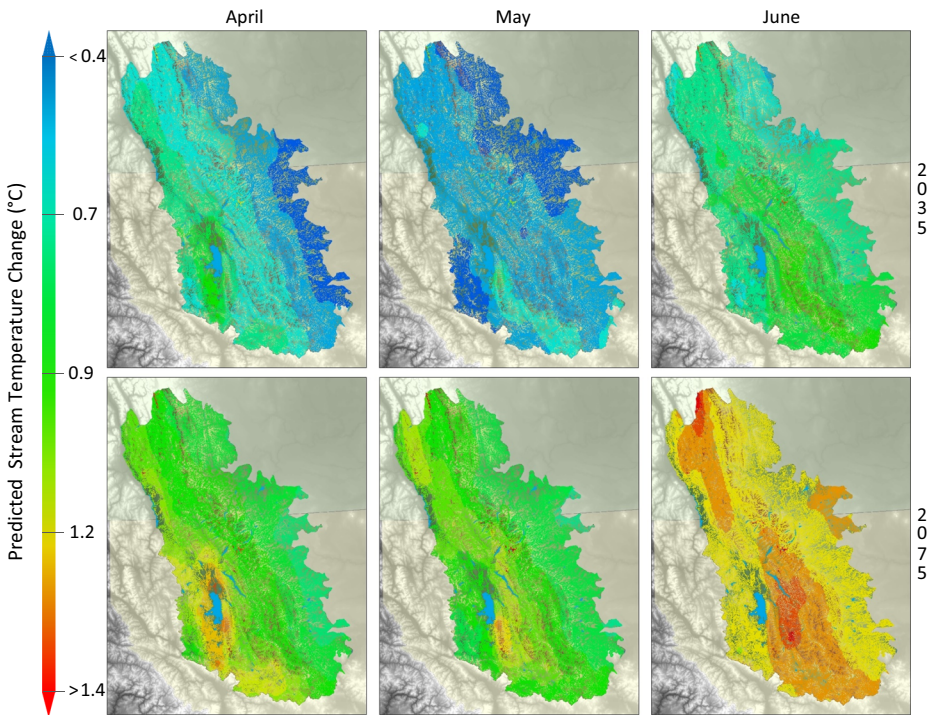


Fig. 3 Predicted absolute stream temperature warming ($^{\circ}\text{C}$) between the baseline and RCP 4.5 scenarios for spring season (April, May, and June)

earlier onset of spring and summer (Pederson et al. 2010). These patterns have led to a narrowing of the winter season and extended duration of the summer season. Our results suggest that similar patterns are expected for stream temperature regimes throughout the CCE. Baseline model simulations show that the warmest average stream temperature conditions are observed during August. Our future model simulations predict that the most significant increases will occur during the summer months, where thermal conditions characteristic of current August regimes are predicted to be exceeded during July and September. These results imply that stream temperatures consistent with current August temperatures are likely to begin a month earlier (July) and persist a month later (September), resulting in an earlier onset and extended duration of warm summer stream temperatures. Seasonal models also predict that forecasted temperature increases during the shoulder seasons of spring and fall (April and November) may be larger in magnitude relative to current conditions, with the most dramatic temperature changes occurring in the seasonal transitions into and out of winter (i.e., shortening of the winter season). These results indicate that future climate warming is likely to result in seasonal shifts in stream temperatures in the CCE, including an earlier onset of temperatures characteristic of spring and summer and later onset of temperatures characteristic of fall and winter.

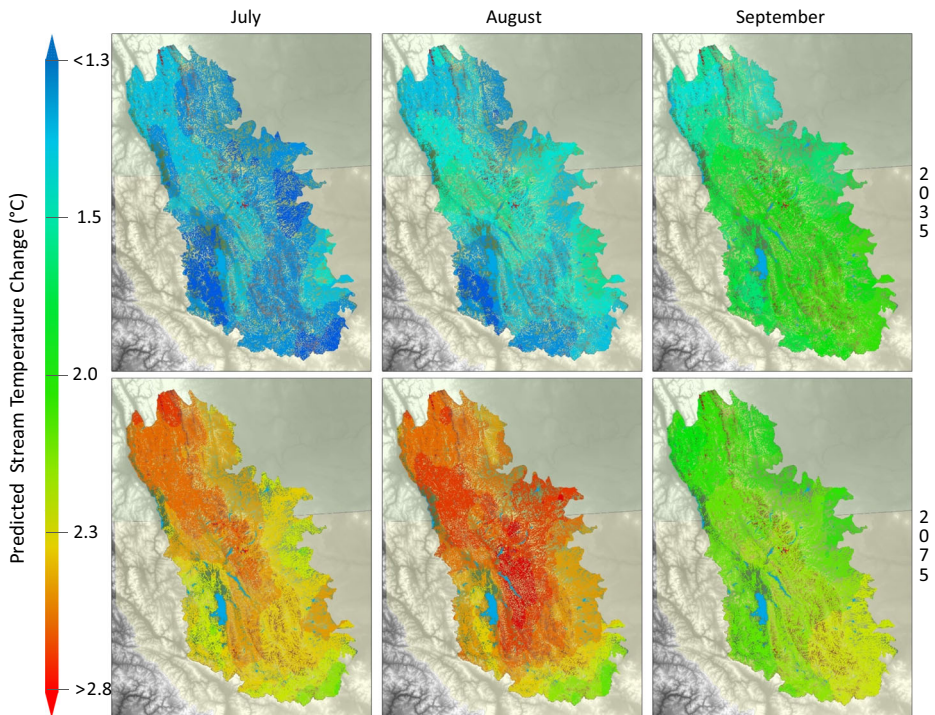


Fig. 4 Predicted absolute stream temperature warming ($^{\circ}\text{C}$) between the baseline and RCP 4.5 scenarios for summer season (July, August, and September)

4.2 Model uncertainty and future research needs

Evaluation of model predictions shows lower uncertainty in the summer and fall models, while variability in spring predictions was relatively high. In snowmelt-driven systems, such as the CCE, annual stream flow regimes are driven by accumulation of winter snowpack, spring precipitation rates, and the seasonal timing of snowmelt (Pederson et al. 2011). Thermal variations during the spring season, therefore, are strongly influenced by hydrologic processes (i.e., snowmelt, rain vs. snow, flow accumulation). The relatively high variation of change (CV) predicted for April indicates some level of uncertainty in the model predictions. The uncertainty is likely a result of stream reach-scale hydrologic influences and thermal variability in surface runoff and tributary inflows. These results may suggest the need for a process-based modeling approach which includes snowmelt runoff during the spring months. Due to the sparse spatial and temporal representation of empirical gage data throughout the ecosystem, we could not incorporate discharge into the models. We did consider the use of precipitation as a proxy for discharge; however because precipitation is not well constrained, for lack of available data, climate model bias and prediction errors are amplified (Allen and Ingram 2002). In addition, due to the transboundary nature and large spatial domain of this ecosystem, hydrologic model predictions (historic and future) were not available. For all models in the study, the largest source of uncertainty is simply how much the Earth's climate will warm and how large-scale changes in the atmosphere will be realized at regional and local scales.

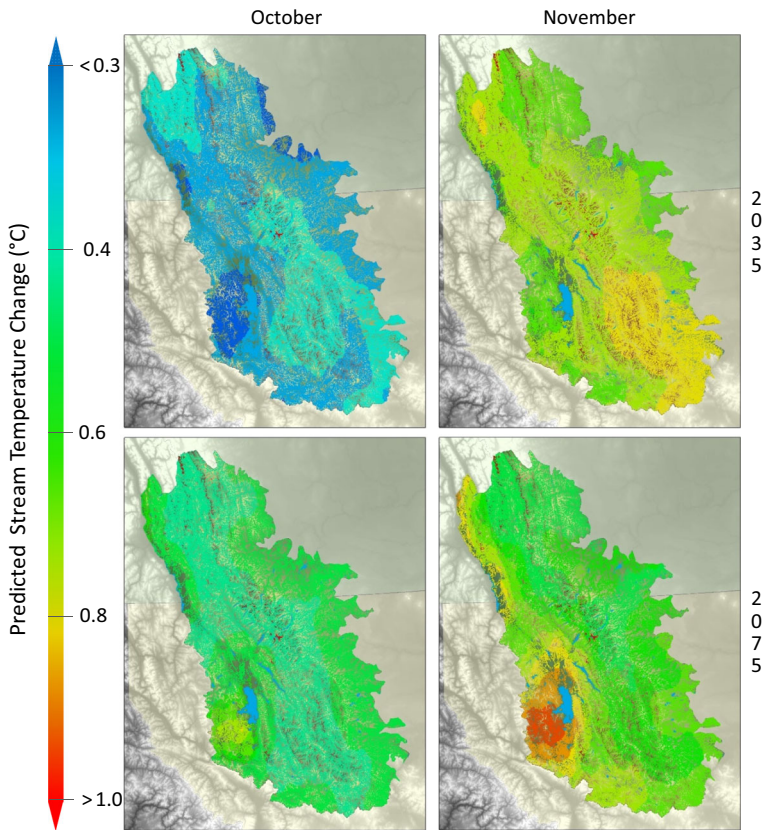


Fig. 5 Predicted absolute stream temperature warming ($^{\circ}\text{C}$) between the baseline and RCP 4.5 scenarios for fall season (October and November)

While statistical models are useful for inferring landscape-scale patterns, incorporating complex physical processes and interactions remains a challenge. Landscape-scale analyses provide insights into the broad patterns of ecosystem response and are useful to describe the relative nature of change across broad geographic areas. However, these approaches generally do not capture thermal variations occurring at the lowest hierarchical levels of stream networks, such as specific habitat units or stream reach scales (i.e., groundwater, riparian shading, channel depth; Snyder et al. 2015). Seasonal model results showed the slope parameter sign change from positive (+) in the spring to negative (–) in the summer and back to positive in the fall. Slope is often used as a proxy for stream order and to describe flow accumulation characteristics in montane ecosystems, where higher slope values represent smaller headwater streams and low slope values represent larger stream and rivers (Isaak et al. 2010). Groundwater discharge has potentially greater impacts in small headwater streams than in larger downstream reaches because of the low volumes of water, therefore, playing an important role in streamflow generation and temperature regulation (Sullivan and Adams 1991). Studies have even used flow-weighted slope as a proxy for describing groundwater contributions and modeling temperature effects (Callahan et al. 2015). The relationship between slope and stream temperature in our model results may reflect a broad characterization

of groundwater contributions in headwater streams, where a cooling effect is observed during the summer months and a warming effect is observed during spring and fall.

Recent studies have questioned the non-stationarity of processes across spatial and temporal domains and scales and have begun to emphasize the importance of geomorphology, hydrology, and physical processes influencing stream temperature variation and the potential of these controls to mediate the sensitivity of thermal warming to climatic changes (Arismendi et al. 2014; Khamis et al. 2015; Lisi et al. 2015). In the application of statistical stream temperature models, the non-stationarity of heat flux process extends to the assumed air-water temperature relationship. However, the strong air-water temperature correlations in our seasonal data show that at broad spatial and temporal scales, this hysteresis is less of a concern. Conversely, increased variability and deviations from regional climate patterns will be amplified as spatial and temporal scales narrow (Letcher et al. 2016). By developing seasonal models, we demonstrate the temporal variability of the air-water temperature relationship and contributing response from second- and third-order parameters across seasons. It is less certain, however, in what manner these relationships may change as models are extrapolated outside the spatial and temporal domains of empirical data (Arismendi et al. 2014).

4.3 Model application

The CCE was recently selected as one of seven *Resilient Landscapes* to highlight landscape-scale management approaches toward building climate resilience through cooperative, inter-agency institutions and partnerships in the USA and Canada (JIWG 2016). This study was developed as part of a decision support framework for setting conservation goals and implementing climate adaptation strategies for conservation of aquatic species and habitats in the CCE. Specifically, we provide a spatial and temporal framework for targeting cold-water refugia and identifying potential shifts in distributions of thermally suitable habitats and life history traits of aquatic organisms. Ectothermic organisms are particularly sensitive to stream temperature warming because thermal distributions within rivers and streams influence physiology, survival, performance, abundance, distribution, and phenology (Schindler 2001). Rising stream temperatures will likely cause the distributions of many species to shift or contract as they differentially track their thermal niches (Isaak and Rieman 2013), and depending on thermal tolerances of a given species may result in increased thermal stress, particularly during the summer months. Thermal changes during spring and fall are likely to drive species response to temperature optimums and thermal cues related to critical life history traits (i.e., reproduction and migration cues). For aquatic species, adaptations to climate-induced stream temperature variations will require phenotypic (short-term) or genetic (long-term) responses based on physiological and behavioral sensitivities to change (Muñoz et al. 2015). Such capacities for adaptation are key determinants of how populations and species can persist into the future. This study provides a useful research and conservation management tool for assessing aquatic species' impacts and vulnerabilities to both short-term and long-term temperature change (Crozier et al. 2008).

Climate in the next century will likely be characterized by shifts in global weather patterns and climate regimes, with increases in average temperatures, changes in precipitation patterns, and increasing incidence of extreme climatic events (IPCC 2013). Our results imply increasing trends in stream temperature warming as compared to historic trends (Isaak et al. 2012). These findings are consistent with exponential increases in seasonal warming (Pederson et al. 2010) and projected atmospheric warming in the CCE (CCCMA 2014; IPCC 2013). However, because stream temperature records are of limited length (i.e., time series) in the CCE, a

comparison of historic and projected warming trends is not feasible. This underscores the importance of long-term monitoring of stream temperatures and freshwater ecosystems (Kovach et al. 2016). More importantly, monitoring within montane systems which are the lifeline of freshwater resources and the world's "water towers" providing essential freshwater for a significant proportion of the growing global population (Viviroli and Weingartner 2004).

Impacts of climate change on plant and animal species and ecosystems can already be observed (Parmesan and Yohe 2003). However, considerable uncertainty remains concerning the extent of change on a regional basis (Harris et al. 2006). For freshwater ecosystems, biotic exchange (i.e., non-native invasions) may be most at risk to climatic change (Sala et al. 2000; Muhlfeld et al. 2014). In the CCE, ecological connectivity is one of the primary factors driving biotic resilience, and both terrestrial and aquatic habitat fragmentations threaten biological diversity. Forecasting biological response to climate change, therefore, plays an important role to informing scientists and decision makers of potential risks and providing a means to support the development of proactive strategies to reduce climate impacts on species and biodiversity. Our models provide spatially explicit forecasts of seasonal stream temperature warming and an important dataset for guiding conservation of freshwater resources in one of the most ecologically intact ecosystems in North America.

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Authors' contribution L.A.J., C.C.M., and L.A.M. designed the study. L.A.J. and C.C.M. collected and assembled the data. L.A.J. performed analysis, modeling, and cartography; L.A.J. and C.C.M. wrote the paper. All authors discussed the results and commented on the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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