Predicting thermal vulnerability of stream and river ecosystems to climate change

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Abstract We use a predictive model of mean summer stream temperature to assess the vulnerability of USA streams to thermal alteration associated with climate change. The model uses air temperature and watershed features (e.g., watershed area and slope) from 569 US Geological Survey sites in the conterminous USA to predict stream temperatures. We assess the model for predicting climate-related variation in stream temperature by comparing observed and predicted historical stream temperature changes. Analysis of covariance confirms that observed and predicted changes in stream temperatures respond similarly to historical changes in air temperature. When applied to spatially-downscaled future air temperature projections (A2 emission scenario), the model predicts mean warming of 2.2 °C for the conterminous USA by 2100. Stream temperatures are most responsive to climate changes in the Cascade and Appalachian Mountains and least responsive in the southeastern USA. We then use random forests to conduct an empirical sensitivity analysis to identify those stream features most strongly associated with both observed historical and predicted future changes in summer stream temperatures. Larger changes in stream temperature are associated with warmer future air temperatures, greater air temperature changes, and larger watershed areas. Smaller changes in stream temperature are predicted for streams with high initial rates of heat loss associated with longwave radiation and evaporation, and greater base-flow index values. These models provide important insight into the potential extent of stream temperature warming at a near-continental scale and why some streams will likely be more vulnerable to climate change than others.

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1 Introduction

Climate change (CC) is expected to have profound effects on stream ecosystems (Woodward et al. 2010). In general, climate is a good surrogate of overall stream heat budgets as evidenced by the strong spatial and temporal association between stream temperature (ST) and air temperature (AT) (Stefan and Sinokrot 1993; Mohseni and Stefan 1999). STs are therefore expected to correlate with future changes in climate. Indeed, numerous observational studies of historical records from around the world confirm that STs have generally followed AT trends over the last century (e.g., Webb 1996; Hari et al. 2006; Chessman 2009; Kaushal et al. 2010). In addition, both empirical (e.g., Mohseni et al. 2003; Isaak et al. 2010) and deterministic (van Vliet et al. 2013) modeling suggests that STs will respond to future CC. However, many of these studies were based on relatively few streams and short periods of record, or included relatively few environmental factors. It is therefore difficult to generalize regarding the potential future extent of ST warming at regional to continental scales, where the most vulnerable streams are, and why some streams are more vulnerable to CC than others. Improving forecasts of the effects of CC on specific stream ecosystems requires that we first understand how the thermal environments of individual streams respond to these changes. We must better characterize how local climates will change at individual streams and how local stream features and processes interact with climate to affect STs.

At least two issues influence how well we estimate the effect of CC on hydrologic systems (Kundzewicz and Stakhiv 2010): local biases and the coarse spatial resolution of general circulation models (GCMs). GCMs were not developed to accurately predict local-scale CC (Wilby 2010). We need finer resolved climate information to predict how individual streams will respond to CC to make better site and region-specific ST projections (Flint and Flint 2012). Ensembles of climate projections can improve accuracy of individual predictions, but such approaches do not address the fact that GCMs are too spatially coarse (~100–300 km) for many hydrologic applications (Solomon et al. 2007). To make better site and region-specific ST projections, we need to reduce uncertainty associated with both simplified model physics and the coarse spatial resolution of GCMs (Caldwell et al. 2009). Spatial refinement of CC projections through dynamical and statistical downscaling could reduce uncertainty associated with both simplified model physics and the coarse spatial resolution of GCMs (Wilby et al. 2000).

The degree to which STs at individual streams will respond to CC depends on several factors, including the balance between heat gains and losses. Previous studies show that streams that experience greater climate warming are more susceptible to ST warming. However, ST vulnerability to CC also depends on river size and the buffering effects of ground-water and shading (O'Driscoll and DeWalle 2006). In addition, the initial, pre-CC, thermal state of a stream should also influence the amount of additional heat it can assimilate. The water surface heat exchange processes that determine STs are: $S_n + A_n - (LWR + C + E)$, where S_n is net solar radiation, A_n is net atmospheric longwave radiation, LWR is longwave back radiation from the water, C is convection/conduction between the air and stream surface, and E is evaporation (after Chapra 1997). Warmer streams experience greater heat loss due to evaporation and longwave radiation, and these losses scale in such a way that they may eventually match heat gains, thereby limiting the warmest temperature a stream can achieve (Mohseni et al. 2002). To understand and forecast ST vulnerability we must understand the relative influence of both exposure and heat loss on ST, and how both processes vary geographically.

Our primary objective was to estimate future effects of CC on the thermal condition of streams within the conterminous USA. To address this objective, we first determined if a

previously developed empirical ST model (Hill et al. 2013) could adequately predict the effects of CC on mean summer ST within the conterminous USA. To predict future STs, we downscaled USA-wide climate projections to improve site-specific predictions of CC. Finally, we conducted a sensitivity analysis of the ST model to determine which stream and watershed features were most strongly associated with climate-related ST vulnerability.

2 Materials and methods

2.1 Overview of data and approach

We conducted two main analyses on three ST datasets (Fig. 1). For the first analysis, we evaluated how well a previously developed, large-scale model of mean summer ST predicted CC-related thermal alterations in USA streams. The ST model was calibrated with recent (1999–2008) ST and climate data (section 2.2). We evaluated the ST model with data at sites for which both historical (1972–1998) ST measurements and climate data (Daly et al. 2008) were available (section 2.3). Model performance was evaluated based on three criteria: (1) how faithfully did the model predict past climate-related changes in ST (henceforth Δ ST), (2) did the model predict past STs with enough precision to detect climate related Δ STs, and (3) over what geographic range within the conterminous USA could these predictions be made with confidence? After evaluating the model, we forecast changes in ST (Δ ST_{Fut}) by applying downscaled AT projections for the beginning (2001–2010) and end (2090–2099) of the 21st century to the ST model (section 2.5). We then conducted a sensitivity analysis (Fig. 1) to determine what stream and watershed features were associated with both observed historical and projected future Δ STs (section 2.6).



Fig. 1 Diagram of datasets and analyses used in this study

2.2 Reference condition ST model

We used a random forest model (Breiman 2001) that we previously developed to predict mean summer (i.e., average of daily STs from July to August) STs under recent climate conditions (1999–2008) (see Hill et al. 2013 for details). Random forest is a non-linear, non-parametric empirical modeling technique that can model continuous data from independent observations, much like regression (Cutler et al. 2007). In addition, random forest ranks the importance of each model predictor by randomly permuting the values of each variable and calculating the percent increase in mean squared error associated with each predictor (Breiman 2001). Model relationships can be interpreted with partial dependence plots, which depict the mean ST response over the complete range of each predictor variable while accounting for the effects of all other predictor variables (Hastie et al. 2001). Random forest has been used for numerous applications recently, including hydrology and water quality monitoring (e.g., Ordoyne and Friedl 2008; Carlisle et al. 2010). We developed the ST model with summer ST data collected from 569 reference-condition (i.e., minimal human-caused stream and watershed alteration, Hawkins et al. 2010) USGS sampling sites. These sites were distributed across the conterminous USA and represented a large range of physical environments and river sizes (e.g., watershed areas of $0.5-100,000 \text{ km}^2$). Reference-quality sites were sparse in regions that were dominated by agricultural land use, but relative to all USGS ST sites, their use for model development did not substantially restrict the environmental conditions over which the model could be applied within the USA (Hill et al. 2013). For each site, we used ST records for single summers because very few USGS sites have long-term temperature data for modeling. When a site had >1 summer of ST records, we randomly selected one summer from 1999 to 2008 for analysis ("Observed" dataset in Fig. 1). We then matched these specific summer ST records with their corresponding mean summer AT (also July-August) and precipitation (annual measure) data derived from 4-km PRISM climate rasters (Daly et al. 2008) to incorporate both spatial and annual variation in STs and climate within the model. In addition to climate, we included 37 other potential stream and watershed features as predictors to provide environmental context and improve both performance and interpretation of the model. These predictors included: geology, hydrology, soils, topography, vegetation, and solar radiation (see Hill et al. 2013 for details of predictor derivations). We then fit a single, nation-wide model to these data by applying variable selection techniques. This final model included six predictors, which in order of importance were mean summer AT (July-August), watershed area, base-flow index (Wolock 2003), mean stream channel slope, soil bulk density (Wolock 1997), and elevation ranges within each watershed. The model predicts STs by accounting for differences in the physical environments among streams. The model explained a large proportion of the observed variance in STs (r²=0.87), was unbiased, and had a root-mean-square error of 1.9 °C (Hill et al. 2013). Notably, AT was the single most important predictor of mean summer ST.

2.3 Assessing the ST model for predicting effects of CC on streams

To evaluate how well our model predicted the effects of CC on STs at individual stream sites, we compared observed changes in historical STs with those predicted by the model (i.e., Δ ST in Analysis 1 of Fig. 1). We applied the same data sufficiency requirements used by Hill et al. (2013) during model development to the historical ST records (1972–1998). One hundred and thirty three sites met these criteria during this period. If a site had multiple years of ST record, we selected the earliest available year and calculated mean summer ST to maximize temporal differences between observations. We then matched the selected site-year ST records with the corresponding site-year PRISM AT climate data and applied the ST model to predict historical

STs. For each site, we calculated Δ ST as the difference between observed current (Obs_{curr}) and observed historical (Obs_{hist}) STs (Fig. 1):

$$\Delta ST_{Obs} = ST_{Obs_{curr}} - ST_{Obs_{hist}} \tag{1}$$

and predicted current (Pred_{curr}) and predicted historical (Pred_{hist}) STs:

$$\Delta ST_{Pred} = ST_{Pred_{curr}} - ST_{Pred_{hist}} \tag{2}$$

We then regressed ΔST_{Obs} and ΔST_{Pred} on ΔAT ($AT_{curr} - AT_{hist}$) for those same years. We used analysis of covariance (ANCOVA) to test for differences in the regression slopes and intercepts of ΔST_{Obs} and ΔST_{Pred} as functions of ΔAT . ANCOVA first tests for differences in the slopes of two regression lines. Similar slopes would indicate that ΔST_{Obs} and ΔST_{Pred} behave similarly in response to ΔAT . If slopes are statistically identical, ANCOVA then tests for differences in the regression intercepts. Different regression intercepts would indicate systematic bias (consistent over or under prediction) in the ΔST_{Pred} response to ΔAT , relative to ΔST_{Obs} . Finally, ANCOVA tests if the slopes of the two regressions lines are different from 0. If the ΔST - ΔAT regression slope is statistically different from 0, the precision of the ST predictions is sufficient to detect climate-related effects on ST given sampling and modeling error.

2.4 Assessing the geographic scope of the ST model under CC

Random forest is a tree-based modeling technique (Breiman 2001), and therefore cannot extrapolate beyond the data range (i.e., model experience) used in model development. We identified regions of the conterminous USA that, by the end of the 21st century (2090–2099), were predicted by the climate forecasts to have AT values outside of the range of AT values used to calibrate the ST model. These regions do not necessarily represent novel AT environments within the conterminous USA, but rather places where future ST projections cannot be made with confidence. We removed these sites from further analyses of CC-related changes in ST and mapped their locations.

2.5 Future climate projections

We used 10-year mean modeled AT values to represent the climate expected for a typical year at both the beginning and end of this century. These AT means were derived from hybrid-downscaled (i.e., dynamically and statistically) climate projections for 2001–2010 and 2090–2099 (Fig. 1). We used one emission scenario and GCM combination rather than an ensemble of AT predictions because dynamically downscaling multiple emission-GCM combinations would have greatly exceeded available time and computational resources. We used the A2 emission scenario with the Community Climate System Model version 3 (CCSM3) GCM (Collins et al. 2006). This CCSM3 scenario was also used in the North American Regional Climate Change Assessment Program (NARCCAP, www.narccap.ucar.edu). We initially selected A2 as the business-as-usual emission scenario, but actual carbon emissions have exceeded those predicted by this scenario (Raupach et al. 2007).

To produce high-resolution (4 km) climate predictions, we first corrected biases in the CCSM3 predictions by regressing CCSM3 predictions for each 150-km cell against corresponding observational data (i.e., globally interpolated National Oceanic and Atmospheric Administration - National Center for Atmospheric Research climate observation data; Kalnay et al. 1996). The data used in these time-series regressions spanned 1969 to 1999. These

regression models were then used to adjust CCSM3 projections on a cell-by-cell basis. Evaluation of a validation data set (2001–2010) showed the statistical adjustments reduced biases and errors relative to original CCSM3 projections for this period. We then used the bias-corrected CCSM3 output as initial and lateral boundary conditions for calibrating the Weather Research and Forecasting (http://wrf-model.org/index.php) regional climate model, which we used to dynamically predict climate at a 50-km spatial resolution across the conterminous USA for 2001–2010 (henceforth 2000s) and 2090–2099 (henceforth 2090s) (see Jin et al. 2011 for methods). These 50-km climate grids were further downscaled to 4 km by creating time-series regressions between regional climate model predictions (50-km) and each of the ~156 4-km PRISM pixels within each regional climate model grid cell for the calibration period (1969–1999). We applied these regressions to each 50-km climate pixel to produce the final spatially-downscaled and bias-corrected monthly climate projections. The 120 monthly-downscaled climate projections for each period (the 2000s and 2090s) were then averaged to estimate mean annual AT characteristics of each decade.

Because of resource constraints we could not use an ensemble of climate models to address uncertainty associated with climate predictions. We therefore compared our predictions for different regions with those of several other GCM-regional climate model models produced by NARCCAP for a similar time period (Appendix). Our projected changes in AT (black circles in Appendix) are similar to the NARCAPP forecasts (red circles in Appendix; Mearns et al. 2013).

2.6 Future ST predictions

We applied the 10-year AT means to each ST model to predict mean summer STs at the beginning and end of the 21st century. To evaluate the use of the downscaled AT projections in the ST model, we compared summer ST predictions made with the downscaled 10-year AT means for the 2000s with predictions made with mean 10-year PRISM ATs for the same period. Spatially-explicit predictions made with the downscaled climate grids closely matched those made with PRISM climate data ($r^2=0.98$, root mean squared error = 0.5 °C), indicating that the downscaled climate projections did not introduce additional bias or error to the ST predictions. We calculated predicted changes in ST over the next century as (Fig. 1):

$$\Delta ST_{Fut} = ST_{Pred_{2000s}} - ST_{Pred_{2000s}}$$
(3)

We also calculated mean, among-site future Δ STs and mapped site-specific changes to explore spatial patterns in ST vulnerability to CC.

2.7 ST vulnerability to CC

We used random forest modeling to conduct a sensitivity analysis to identify those ST predictors most strongly associated with Δ STs. We developed two models based on two datasets of estimated Δ ST. The first dataset consisted of measured historical Δ ST (i.e., Δ ST_{Obs} in Fig. 1 and Eq. 1) based on the 133 summer ST sites with data prior to 1999. The second dataset included predicted future Δ STs (Δ ST_{Fut} in Fig. 1 and Eq. 3) from the USGS sites that were used to calibrate the original summer ST model and were also predicted to be within the experience of the ST model at the end of the 21st century. The first dataset (Δ ST_{Obs}) was smaller, but consisted of measured ST values. The second dataset (Δ ST_{Fut}) had a larger sample size and greater range of environmental conditions, but consisted of predicted ST values. Consistency between the two models would provide confidence in the Δ ST_{Fut}

sensitivity analysis and in the factors identified as important to ST vulnerability (i.e., the Δ ST_{Obs} model is a validation of the Δ ST_{Fut} model). For the sensitivity analysis, we tested predictor variables that were used in the original summer ST model (see section 2.2): watershed area, base-flow index, stream slopes, soil bulk density, and elevation ranges within each watershed. In addition, we included two aspects of AT that represented (1) the potential future exposure to climatic forcings that influence ST and (2) changes in exposure from initial conditions, i.e., predicted future AT and changes in AT at each site.

For each Δ ST model, we also estimated the vapor pressure deficit (a major component of evaporative heat loss) and longwave radiation emitted by each stream at the beginning of each model period. For example, we estimated these energy losses during the 2000s to represent the initial thermal states of streams for use in the sensitivity analysis of Δ ST_{Fut}. We estimated potential evaporative heat loss from empirical relationships between vapor pressure and ST and PRISM dew point temperature (Chapra 1997):

$$VPD = 4.59e^{\frac{17.27ST}{237+ST}} - 4.59e^{\frac{17.27DPT}{237+DPT}},$$
(4)

where VPD is the vapor pressure deficit (kPa) at the air-water interface, and DPT is the PRISM air dew point temperatures (°C) at each site. We used the Stefan-Boltzmann law to approximate differences in longwave radiation among sites based on the initial measured ST as:

$$LWR = \varepsilon \phi (ST + 273)^4, \tag{5}$$

where LWR is the longwave radiation emitted by a stream (Wm⁻²), ε is the emissivity of water (~0.97), and ϕ is the Stefan-Boltzmann constant (5.67×10⁻⁸ Wm⁻² K⁻⁴). Vapor pressure deficit and longwave radiation are important components of stream heat budgets, and we included them in the sensitivity analysis to potentially improve our understanding and interpretation of why some streams are more vulnerable to CC than others. We selected predictors by sequentially adding variables to the model if they both improved the random forest pseudo r-squared value by ≥4 points and had Pearson correlations (r)≤|0.60| with predictors already in the model to minimize redundancy between predictors. Random forest modeling is resistant to correlations among predictors (Breiman 2001), but we removed strongly correlated predictors to improve model parsimony and interpretation. For each selected predictor, we then created a partial dependence plot to interpret its association with Δ ST. To facilitate comparisons between the observed historical Δ ST and predicted future Δ ST models, we standardized Δ STs in both datasets to have means=0 and standard deviations = 1. We also created ranked lists of the importance of each predictor in explaining variation in Δ ST.

3 Results

3.1 Evaluation of the ST model for CC studies

ANCOVA showed that ΔST_{Obs} and ΔST_{Pred} responded similarly to ΔAT . The slopes for the regressions of ΔST_{Obs} and ΔST_{Pred} on ΔAT were not significantly different from each other (Table 1), indicating observed and modeled ΔSTs responded to ΔAT in a similar (statistically indistinguishable) way. However, the regression intercepts were different from one another showing that the model (ΔST_{Pred}) under predicted changes in summer STs to historical changes in AT by 0.49 °C on average (Table 1). The predictions of CC-related effects on

Model	Param. Estimate	Std Error	t	<i>p</i> -value
Test for difference in slopes				
Intercept	0.58	0.11	5.50	< 0.001
ΔAT	0.42	0.07	6.10	< 0.001
ObsVsPred	-0.55	0.15	-3.71	< 0.001
$\Delta AT x ObsVsPred$	0.11	0.10	1.19	0.237
Test for difference in means				
Intercept	0.55	0.10	5.37	< 0.001
ΔAT	0.47	0.05	9.78	< 0.001
ObsVsPred	-0.49*	0.14	-3.52	< 0.001

Table 1 Analysis of covariance (ANCOVA^a) of observed and predicted (ObsVsPred) changes in mean summer stream temperatures versus observed changes in air temperature (ΔAT)

^a ANCOVA first checks for statistically significant differences in slopes (p<0.05) between observed and predicted STs (significant Δ AT x ObsVsPred interactions). If none is found, it then checks for significant differences in regression intercepts, i.e., adjusted means (ObsVsPred). Where differences in intercepts are detected, the parameter estimate of ObsVsPred represents the bias associated with predicted Δ ST (value marked with "*"). Statistically significant relationships were also observed between Δ AT and Δ ST in each model

STs will therefore likely be conservative. Although the variance explained in the regression models was low for ΔST_{Obs} ($r^2=0.15$, cf. r^2 for $\Delta ST_{Pred}=0.53$), ΔSTs in both models were positively and statistically significantly associated with ΔATs (Table 1), indicating that model precision was sufficient to detect climate-related variation in STs given observation and modeling error.

3.2 Geographic scope of the ST model under future climatic conditions

Over 92 % of predicted future ATs were within the range of values (i.e., model experience) used to calibrate the ST model. Just 18 ST calibration sites were predicted to have AT conditions outside of the range of calibration temperatures by the 2090s. These sites fell within Florida, Texas, and Nevada (sites identified with "Xs" in Fig. 2). Removal of these sites resulted in 551 sites that we used to make mean summer ST projections to the 2090s.

3.3 Climate and ST projections

ATs at study sites were projected to warm by 4.0 °C on average over the next century. In response to these changes in AT, the ST model predicted average warming of 2.2 °C for summer STs, i.e., a warming of 0.6 °C (s.d.=0.3) Δ ST per 1 °C Δ AT. Values of predicted future Δ STs varied greatly among individual sites (Δ ST=0 °C to +6.2 °C). The model predicted greatest summer ST warming in the Pacific Northwest and the central and northern Appalachian Mountains (Fig. 2). For example, the ST model predicted average warming of 3.0 °C for streams in the Cascade Mountains of Oregon (Δ ST/ Δ AT=0.82), but 22 % of those sites were predicted to experience warming \geq 4 °C. Likewise, the model predicted average warming of 2.3 °C for the northern Appalachian Mountains (Δ ST=+1.8 °C) and Southern Appalachian Mountain (Δ ST=+1.6 °C) streams generally had smaller predicted average warming in response to CC (Δ ST/ Δ AT=0.48 and 0.41, respectively). The Southeastern USA was predicted to be the least responsive to CC (Δ ST=+1 °C, Δ ST/ Δ AT=0.27).



Fig. 2 Predicted changes in summer stream temperatures between the 2000s and the 2090s. Black zones and Xs represent regions and USGS ST sites with predicted future air temperatures beyond the range of PRISM climate data used to develop the original ST model

3.4 Vulnerability of STs to CC

We identified several stream and watershed features associated with ST vulnerability for both model eras (historical and future) (Fig. 3). AT at the end of the model period was the most important predictor of ΔST_{Fut} . In contrast, ΔAT was the most important predictor of ΔST_{Obs} , but was also the 2nd most important predictor of ΔST_{Fut} (Fig. 3). In both models, vapor pressure deficit and longwave radiation were also identified as important predictors of ΔST_s . Base-flow index and watershed area were both only selected for the ΔST_{Fut} model, but base-flow index was the third most important predictor. ΔST_{Fut} had a higher random forest pseudo r-squared value (0.81) than ΔST_{Obs} (0.25).

The direction of association for most predictors was similar between the two models of Δ ST (Fig. 4). Δ ST_{Obs} showed a consistent positive association with ATs in the 2000s (grey with black dashed lines in Fig. 4). However, the association between Δ ST_{Fut} and predicted ATs for the 2090s was unimodal (black line in the "AT_{Fut}" plot of Fig. 4) and was the only relationship that was not generally consistent between eras. Historical and future Δ STs were positively associated with greater Δ AT, whereas Δ ST was always negatively associated with initial longwave radiation and vapor pressure deficit at study sites (Fig. 4). Δ ST_{Fut} had a slight negative association with increasing base-flow index values and positive association with increasing watershed area.

4 Discussion

This study provided new insight regarding how CC will likely affect STs over the 21st century at the scale of the conterminous USA. However, it is important to place our study in context



Fig. 3 Importance (% increase in mean squared error of the model when the predictor is not included) of the predictor variables for both historical (*triangles*) and future (*circles*) stream temperature vulnerability models. Abbreviations in figure: ΔAT change in historical PRISM or predicted future air temperature from current (2000s) conditions, AT_{fut} future air temperature observed (PRISM in 2000s) or predicted (2090s) to occur relative to the initial time period used to develop the ST vulnerability measures, *LWR* initial longwave radiation, *VPD* initial vapor pressure deficit at the air-water interface of each stream, *WA* watershed area, *BFI* base-flow index

with other CC-ST studies and consider whether our results represent plausible responses of ST to CC. In addition, we discuss the challenges that differences in ST vulnerability pose to



Fig. 4 Partial dependence plots showing the relationship between historical (*grey with black dash*) and predicted future (*black*) stream temperature (*ST*) vulnerability and predictor variables (see Eqs 1 and 4 for the definitions of ST vulnerability used here). ST vulnerability values were standardized to have mean=0. Additional abbreviations in figure: ΔAT change in historical PRISM or predicted future air temperature from current (2000s) conditions, AT_{fut} future air temperature observed (PRISM in 2000s) or predicted (2090s) to occur relative to the initial time period used to develop the ST vulnerability measures, *LWR* initial longwave radiation, *VPD* initial vapor pressure deficit at the air-water interface of each stream, *WA* watershed area

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CC-related ST effects and mitigation given the differences in ST vulnerability we observed. The consistency of our results with previous studies improves confidence in our projections and adds to the growing weight of evidence that streams differ in their vulnerability to CC. For example, in an observational study, Kaushal et al. (2010) estimated long-term mean annual ST warming rates of 0.009–0.077 °C yr⁻¹ in streams that were distributed across the conterminous USA. Eighty-seven percent of our ST sites were predicted to have warming rates within this range. Using regression techniques, Isaak et al. (2010) estimated warming rates of 0.021 °C yr⁻¹ for mean summer ST and 0.026 °C yr⁻¹ for ST maxima from 1993 to 2006 within the Boise River, Idaho. For this same period, our summer ST model predicted a warming rate of 0.027 °C yr⁻¹ for USGS sites within and near the Boise River. Also, the global-scale deterministic model of van Vliet et al. (2013) predicted ST warming within the Mackenzie and Rio Grande River basins by the end of the 21st century of 2.2 °C and 1.4 °C, respectively, which were similar to our predictions (Mackenzie = 2.4 °C, and Rio Grande = 1.0 °C). However, important differences also existed between the two sets of projections. Our model predicted mean summer STs to be less sensitive within the Colorado River basin (+1.9 °C vs. +2.6 °C) but more sensitive within the Columbia River basin (+2.8 °C vs. +1.9 °C) than was predicted by van Vliet et al. (2013). Nonetheless, the general consistency between our ST predictions and those of others support an interpretation that the ST projections we describe here are realistic and plausible.

The effects of CC on STs will pose serious challenges for freshwater resource managers. Changes of 2–5 °C in ST can have substantial effects on stream biota (Sweeney 1993; Hawkins et al. 1997; Chessman 2009) and our model predicted that by 2100, 52 % of the sites we assessed will warm by ≥ 2 °C. Moreover, the ST changes we predicted are similar to or greater than ST alterations associated with past and current land use. For example, Hill et al. (2013) showed that sites in watersheds with urban development were thermally altered by + 0.6 °C to +0.9 °C on average. In other words, over the 21st century, summer STs could be influenced by CC more than they have been affected to date by urbanization. Given the degree of warming predicted by our ST model and the thermal sensitivity of stream biota (Vannote and Sweeney 1980) it is likely that CC will substantially alter the biological composition of USA streams and rivers over the next century. Furthermore, unlike other types of humancaused, environmental alteration, CC will affect both pristine and altered streams alike, and it will be a major challenge to untangle CC-ST interactions from other human-related activities. It is increasingly important to understand the spatial variation in ST responses to CC at large scales and the effects these changes will have on stream biota (e.g., Mohseni et al. 2003).

When designing mitigation and adaptation strategies, we must both recognize that some streams will likely be more thermally vulnerable to CC than others and understand why such differences occur. We identified several factors that may exacerbate or moderate ST responsiveness to CC that may help us understand and predict how streams will respond in the future. For example, the consistent and strong importance of changes in AT underscores the need for unbiased, appropriately resolved climate predictions for understanding how the response of individual streams to changing atmospheric conditions will vary spatially. Likewise, it will be important to clarify how ST vulnerability is affected by future AT exposure. We are unsure why responses of Δ ST_{Fut} to future ATs were unimodal (Fig. 4), but this response may be a consequence of the decreasing sensitivity of ST to AT as ATs increases (e.g., Mohseni et al. 2002). The model of Hill et al. (2013), which is the basis our ST projections, exhibited an s-shaped relationship between ST and AT that implied that upper ST warming may be constrained by heat loss experienced by warm streams. Our models also indicated that ST vulnerability increases slightly with watershed area. This pattern has also been observed by

several others and has been attributed to greater correspondence between STs and ATs in larger rivers caused by the accrual of heat through non-advective processes at the water surface (O'Driscoll and DeWalle 2006; Kelleher et al. 2012; Chang and Psaris 2013) and greater thermal inertia that limits the effects of local factors, such as vegetation (Caissie et al. 2001). Brown and Krygier (1970) noted that ST responsiveness in logged watersheds was a function of the water surface area-discharge ratio, with larger ratios resulting in more responsive streams. The surface area-discharge ratio is generally positively correlated with watershed area (Leopold et al. 1964), hence we should expect that STs would more closely approach ATs as the surface area increases over which heat exchange occurs relative to water volume.

We also showed that the current thermal state of a stream can significantly affect its vulnerability to CC. The likely effect of vapor pressure deficit and longwave radiation on ST vulnerability was well illustrated in Coastal and Cascade Mountain streams of Oregon and Washington (Fig. 2). These streams were especially responsive to projected CC despite being predicted to experience end of the century $\Delta ATs \sim 1.0$ °C cooler than the national average. Cold water streams with atmospheric conditions that have thus far limited heat loss through evaporation will likely experience the most substantial responses in ST. Note, though, that we treated vapor pressure deficit as a fixed factor, but it will also be affected by CC. We therefore need to improve our understanding of how site-specific air and water vapor pressures will change under CC and interact to better determine ST vulnerability. Deterministic simulations of streams across a range of environmental conditions should be especially useful in this regard.

Of the factors that affected ST vulnerability, base flow, the contribution of groundwater to stream flow relative to other sources, has the most potential for management. The constancy of groundwater flow and temperature is an important buffer to the heat exchange processes that occur at the stream surface (Bogan et al. 2003). We treated the base-flow index as a fixed variable within the model, an assumption that may only be robust over moderate time scales given that groundwater temperatures will eventually increase in response to long-term mean AT (Kurylyk et al. 2013). Nonetheless, maintaining groundwater flow to streams will likely be an important moderate-term mitigation and adaptation strategy for minimizing ST changes.

5 Conclusions

Given the tendency of our model to slightly under predict ST response to CC and the specific emission scenarios explored here, it is possible that our results are conservative and that STs will increase even more than we predicted. Despite these potential uncertainties, our analyses provide important insight regarding the likely context-dependencies of ST response to CC. A major advantage of the modeling approach we used is that it can make ST predictions to unmeasured streams. Biological samples are often taken from such streams and few studies have, therefore, examined the potential macro-scale responses of stream biota to CC (Mohseni et al. 2003). Those studies that have done so often do not predict future STs explicitly. Our model should prove helpful in guiding future research into the potential macro-scale ecological effects of CC on the Nation's rivers and streams.

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