



# Elevation-dependent warming of streams in mountainous regions: implications for temperature modeling and headwater climate refugia

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## ABSTRACT

Climate change is warming stream temperatures with significant implications for species that require cold temperatures to persist. These species often rely on headwater habitats in mountainous regions where elevation gradients in hydroclimatic conditions may induce differential patterns of long-term warming that affect the resistance of refugia. Forecasts from mechanistic and statistical stream temperature models diverge regarding whether this elevation dependence will cause above- or below-average warming in headwaters during warm summer periods, so we examined monitoring records for stream temperature ( $n=271$ ), air temperature ( $n=690$ ), and stream discharge ( $n=131$ ) across broad elevation gradients in a mountainous region of western North America to better understand potential future trends. Over a 40-year period characterized by rapid climate change from 1976–2015, air temperature stations exhibited below-average warming rates at high elevations while stream discharge declined at above average rates. Between climatically extreme years that involved summer air temperature increases  $>5^{\circ}\text{C}$  and discharge declines  $>70\%$ , temperatures in high-elevation streams exhibited below average increases but otherwise showed negligible elevation dependence during intermediate climate years. In a subsequent example, it was demonstrated that elevation dependent stream warming has a minor effect on the amount of thermal habitat loss relative to the average water temperature increase within a mountain river network. We conclude that predictions of above average warming effects on headwater organisms for this region may be overly pessimistic and discuss reasons why different types of temperature models make divergent forecasts. Several research areas warrant greater attention, including descriptions of elevation-dependent patterns in other regions for comparative purposes, examination of long-term stream temperature records to understand how sensitivity to climate forcing may be evolving, use of new data sources to better represent key processes in temperature models across broad areas, and development of hybrid models that integrate the best attributes of mechanistic and statistical approaches.

## RÉSUMÉ

Le changement climatique réchauffe les températures des cours d'eau avec des implications importantes pour les espèces qui ont besoin de températures froides pour persister. Ces espèces dépendent souvent des habitats d'amont dans les régions montagneuses où les gradients d'altitude dans des conditions hydroclimatiques peuvent induire des modèles différentiels de réchauffement à long terme qui affectent la résistance des refuges. Les prévisions des modèles mécanistes et statistiques de température des cours d'eau divergent quant à savoir si cette dépendance à l'altitude entraînera un réchauffement supérieur ou inférieur à la moyenne dans les eaux d'amont pendant les périodes estivales chaudes, nous avons donc examiné les dossiers de surveillance de la température des cours d'eau ( $n = 271$ ), de la température de l'air ( $n = 690$ ) et du débit des cours d'eau ( $n = 131$ ) à travers de larges gradients d'altitude dans une région montagneuse de l'ouest de l'Amérique du Nord afin de mieux comprendre les tendances futures potentielles. Sur une période de 40 ans caractérisée par des changements climatiques rapides de 1976 à 2015, les stations de température de l'air ont affiché des taux de réchauffement inférieurs à la moyenne à haute altitude, tandis que le débit des cours d'eau a diminué à des taux supérieurs à la moyenne. Entre les années climatiquement extrêmes qui impliquaient des augmentations de la température de l'air en été  $>5^{\circ}\text{C}$  et des baisses de débit  $>70\%$ , les températures dans les cours d'eau en haute altitude ont montré des augmentations inférieures à la moyenne, mais ont autrement montré une dépendance négligeable à l'altitude au cours des années climatiques intermédiaires. Dans un exemple ultérieur, il a été démontré que le réchauffement des cours d'eau dépendant de l'altitude a un effet mineur sur la quantité de perte d'habitat thermique par rapport à l'augmentation moyenne de la température de l'eau dans un réseau de rivières de montagne. Nous concluons que les prévisions des effets du

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réchauffement supérieur à la moyenne sur les organismes d'amont pour cette région peuvent être trop pessimistes et discutons des raisons pour lesquelles différents types de modèles de température font des prévisions divergentes. Plusieurs domaines de recherche méritent une plus grande attention, y compris la description des modèles dépendant de l'altitude dans d'autres régions à des fins de comparaison, l'examen des enregistrements de température des cours d'eau à long terme pour comprendre comment la sensibilité au forçage climatique peut évoluer, l'utilisation de nouvelles sources de données pour mieux représenter les processus clés dans les modèles de température dans de vastes zones, et l'élaboration de modèles hybrides qui intègrent les meilleurs attributs des approches mécanistes et statistiques.

## Introduction

Global climate change is warming Earth's rivers and streams (Arora, Tockner, and Venohr 2016; Chen et al. 2016; Isaak et al. 2018a; Michel et al. 2020) and poses risks to cold-water species, fisheries, and biodiversity that society values (Reist et al. 2006; Heino et al. 2009; Myers et al. 2017; Barbarossa et al. 2021). In mountainous regions, headwater areas have emerged as important climate refugia for many native aquatic species because of their perennially cold environments and slow rates at which isotherms shift upstream to affect the distribution of thermal habitats (Loarie et al. 2009; Isaak et al. 2016). Mean annual temperatures within many temperate zone montane streams, for example, average 2–6 °C, short-term summer maxima may rarely exceed 12 °C (Khamisa et al. 2022), and isotherms are shifting upstream at only 0.3–1.0 km/decade (Isaak and Rieman 2013; Isaak et al. 2016). A variety of stenothermic fish, insect, mussel, and amphibian species complete their life cycles within these cold habitats (Hotaling et al. 2017; Troia et al. 2019), while other species depend on them for reproduction due to the restrictive thermal requirements that maturing adults and embryos have in comparison to other life stages (Isaak et al. 2015; Dahlke et al. 2020).

As climate change continues, accurate forecasts of water temperatures ( $T_w$ ) throughout river networks in mountainous regions will be vital to biological risk assessments and efficient planning for conservation and watershed restoration. Mountain environments, however, present challenges for stream temperature modeling due to their complex topography, strong environmental gradients, and abrupt discontinuities in factors that affect heat budget dynamics. Headwater streams are also strongly disequilibriumal with flow emerging at local groundwater temperatures from numerous seeps and springs adjacent to low-order channels and then warming along the downstream flow path as the proportional contribution of groundwater inputs decreases (Brown et al. 2003; Kelleher

et al. 2012; Kaule and Gilfedder 2021). Early  $T_w$  forecasts were restricted to stream locations where monitoring occurred and were based on simple statistical approaches that correlated air temperature (AT) variability with  $T_w$  (Stephan and Sinokrot 1993; Eaton and Scheller 1996). But as an early dearth of  $T_w$  records (Ward 1985) has given way to an abundance of data from inexpensive sensors and remote sensing sources (Dugdale et al. 2019; Ouellet et al. 2020), researchers have developed more sophisticated statistical and mechanistic  $T_w$  models capable of predicting thermal conditions at unsampled locations and translating outputs from Global Climate Models (GCMs) to network scale temperature responses that are of greater utility for ecological assessments (Benyahya et al. 2007; Gallice et al. 2015; Dugdale et al. 2017; Wanders et al. 2019).

Statistical models link  $T_w$  observations via probabilistic equations to covariates that are derived from geospatial data sources and hydroclimatic monitoring stations (e.g., stream discharge (Q) gages and weather stations), and which are used as proxies to represent heat budget processes. These covariates are readily quantified from broadly available data sets, which enables integration with large numbers of  $T_w$  observations and model applications across geographically extensive areas (Jackson et al. 2018; FitzGerald et al. 2021; Beaufort et al. 2022). Mechanistic models, by contrast, incorporate direct calculations of stream heat budget components to deterministically predict thermal dynamics in flowing waters. Obtaining measurements of key processes is often challenging and the models are more computationally intensive, which limits the number of  $T_w$  sites where calibration occurs, as well as the scale at which mechanistic models have traditionally been applied (Caissie et al. 2006; Wanders et al. 2019). Mechanistic models offer the advantages of transparent process conceptualization and, it has been argued, are better choices for climate forecasts because of an ability to address interactions among physical processes, potential nonstationarities,

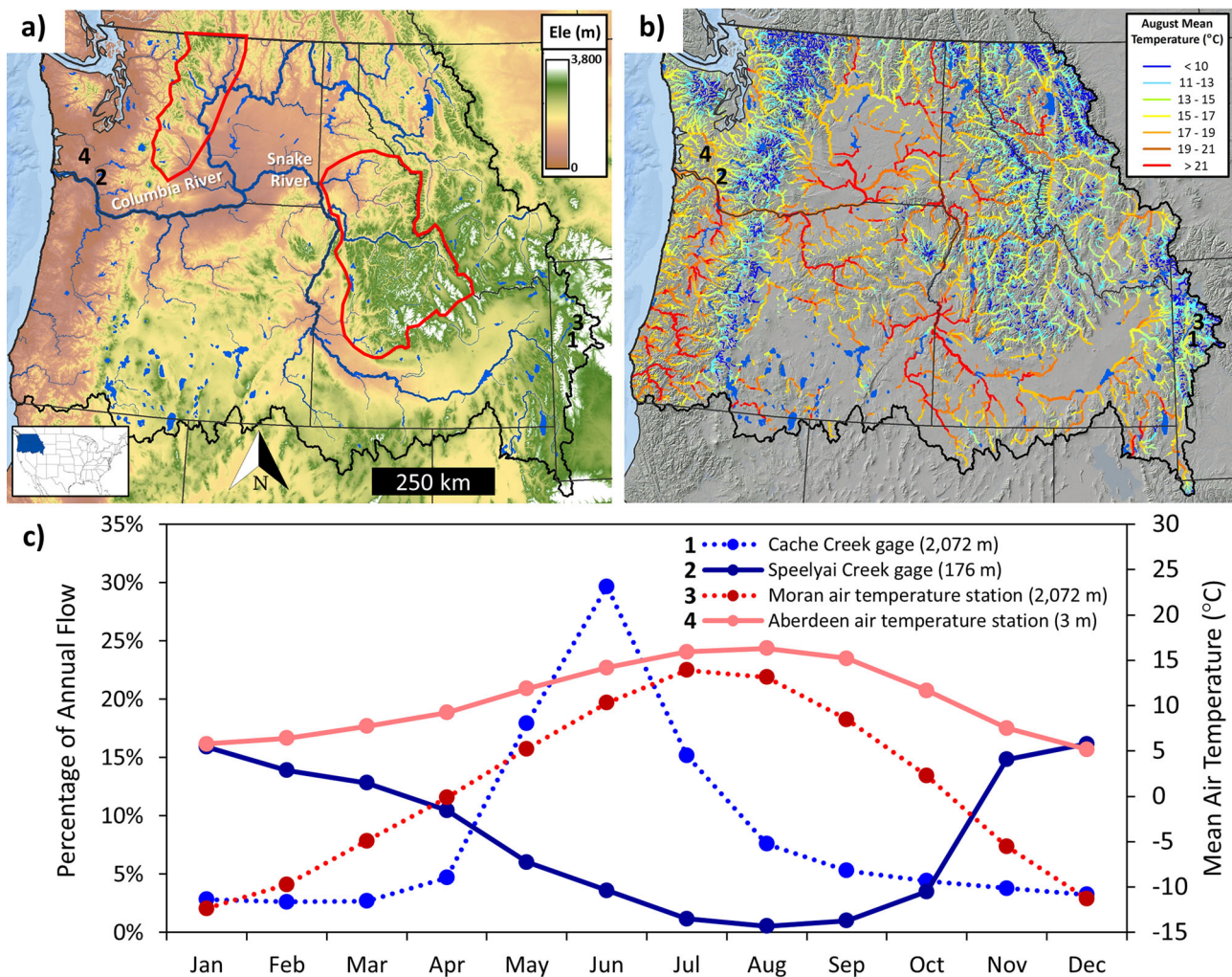
and nonlinear  $T_w$  responses (Arismendi et al. 2014; Leach and Moore 2019).

As  $T_w$  model forecasts have become more common in mountainous areas, an interesting dichotomy has emerged wherein mechanistic models often predict positive elevation-dependent warming (EDW) of streams (i.e., greater warming at high elevations; Wu et al. 2012; Ficklin et al. 2014; Yan et al. 2021; Michel et al. 2022) while statistical techniques sometimes predict negative EDW due to the reduced sensitivity of many headwater streams to climatic variation (Luce et al. 2014; Isaak et al. 2016; Beaufort et al. 2020). Discrepancies between the two model types are not small within the same region, with mechanistic models predicting that high elevation streams may warm 100–200% more than low elevation streams in contrast to a smaller opposing pattern predicted by statistical models in which the coldest streams warm 20–40% less than their low elevation counterparts (Wu et al. 2012; Ficklin et al. 2014; Isaak et al. 2017). Several factors intrinsic or extrinsic to models could account for these differences. For example, inadequate calibration of models to  $T_w$  monitoring sites or records which encompass limited climatic variability and stream environments could result in poor parameterization and predictive forecasts. Luce et al. (2014) have also suggested that the equilibrium formulations used by some mechanistic models (e.g., Null et al. 2013; Ficklin et al. 2014) may be overly prescriptive for the disequilibrium conditions characteristic of mountain streams and could result in overestimation of future temperatures at high elevations. Conversely, Leach and Moore (2019) contend that increasing groundwater temperatures and the thermal memory of catchments may lead to underestimates of future temperature increases by statistical models which do not account for these processes.

Less appreciated in  $T_w$  modeling efforts are trends in external factors that set boundary conditions such as the enhanced warming of AT at high elevations in many mountain ranges (Rangwala and Miller 2012; MRI 2015). Inconsistencies in this pattern are common, however, with some mountainous regions exhibiting negative EDW or no elevation dependency (Pepin et al. 2022). Regardless, because AT is physically linked to stream temperatures through longwave radiation and sensible heat transfer (Leach and Moore 2010; St-Hilaire et al. 2021), the AT-elevation trends that are manifest within a region will have a similar forcing effect on  $T_w$ . Elevation-dependent trends in precipitation and stream Q are also widely reported (Stewart 2009; Pepin et al. 2022) and likely to affect

long-term  $T_w$  responses because flow volumes and velocity determine the thermal capacity of streams and responsiveness to ambient climatic conditions (Gu et al. 1998; Webb et al. 2003; Van Vliet et al. 2011). Similar to the uncertainty associated with AT trends, Q trends vary geographically and high-elevation streams may exhibit above- or below-average changes in summer Q depending on the regional importance of glaciers, snowmelt runoff, and whether total annual precipitation is increasing or decreasing (Moore et al. 2009; Luce et al. 2013; Michel et al. 2020). Lastly, ongoing declines in mountain snowpacks where winter AT values approach the freezing threshold and transitions occur from snow to rain (Stewart 2009; Mote et al. 2018) may reduce the strength of the advective cooling effect that melting snowpacks provide to headwater streams during spring runoff and into the summer (Caissie and Luce 2017; Siegel et al. 2022).

If left unresolved, the discrepancy in EDW predictions among  $T_w$  models for river networks could add to the significant uncertainties already associated with future climate change and potentially sow confusion among conservation practitioners. In fact, recent studies have expressed concern that if positive EDW of headwater streams occurs, it may reduce their effectiveness as climate refugia (Steel et al. 2019; Cline et al. 2020). The more general point, however, is that the use of inaccurate  $T_w$  forecasts could result in the misallocation of investments to mistakenly protect or leave unprotected streams that may serve as climate refugia for sensitive cold-water species. To address the issue of stream EDW, we examined the historical evidence for elevation dependency using long-term monitoring datasets of climate forcing factors across a broad elevation range in a mountainous region of western North America and describe short-term variation in  $T_w$  lapse rates observed during strongly contrasting climatic conditions that provide analogues for future climate change. Through a subsequent example, we compare how positive and negative EDW of streams could affect the extent of thermally suitable habitat for headwater organisms within a river network. Finally, we discuss the factors affecting elevation dependent stream warming, its potential geographic extent and ecological ramifications, and, within the spirit of this special issue, provide a perspective on the relevance of our results for  $T_w$  modeling and important areas of future research. Throughout, a focus is placed on the warm summer months that are most challenging for cold-water organisms in temperate to subarctic zones and which



**Figure 1.** Topography and major rivers in the northwestern U.S. where historical records for air temperature, stream discharge, and water temperature (basins inside red boundaries) were examined for evidence of elevation-dependent trends (a). Perennial stream network (b) showing a mean August stream temperature scenario for the period of 1993–2011 developed from observations at 16,388 unique sites by Isaak et al. (2017). Characteristic annual cycles in stream discharge and air temperature observed at high- and low-elevation monitoring sites (c). Source: Authors.

have been the focus of most efforts to develop  $T_w$  models for ecological applications.

## Methods

### Study area

We studied a 750,000 km<sup>2</sup> mountainous region in the northwestern U.S. which is physiographically similar to the provinces of British Columbia and Alberta immediately to the north (Figure 1). The study area hosts the same cadre of cold-water salmon, trout, and char species that are of conservation concern in western Canada, and which provide much of the motivation for monitoring and modeling stream and river temperatures in the region. Unlike areas north of the international border, however, the northwestern U.S. is particularly rich in hydroclimatic data sets useful

for a retrospective analysis of stream EDW. Numerous studies also document the effects of climate change within the region during past decades (Luce and Holden 2009; Abatzoglou, Rupp, and Mote 2014; Mote et al. 2018), so available instrumental records should contain characteristic signatures that may be indicative of future trends. Projections vary among GCMs that have been run for the region but suggest a range of AT increases between 2°C and 6°C warmer by the end of the century (Abatzoglou and Brown 2012; Hamlet et al. 2013; USGCRP 2018) with attendant hydrological changes that include more precipitation falling as rain rather than snow, earlier snowmelt and stream runoff, and summer low flow periods that are longer and more extreme with declines of 20–80% predicted (Wu et al. 2012; Yan et al. 2021; Tonina et al. 2022).

Two north-south trending mountain ranges dominate the study area, the Cascade Range near the Pacific Ocean where peak elevations are usually less than 2,000 m and the Rocky Mountains further east where elevations often reach 3,800 m (Figure 1). Because of the proximity to the ocean, the Cascade Range experiences a wetter, maritime climate with greater annual precipitation amounts compared to the more continental Rocky Mountains (Daly et al. 2008). In both areas, however, orographic effects create positive elevation trends in annual precipitation amounts (Luce et al. 2013). Most precipitation occurs from October through May and snowpacks accumulate when and where AT persists below 0°C. Peak annual flows occur in low elevation stream drainages with the advent of the wet season in the fall but are delayed at high elevations until the following spring when increasing AT melts snowpacks. Streams and rivers draining the region constitute a perennial network 220,000 km in length and temperature patterns during warm months progress from cold mountain headwaters where averages are often < 8°C to warm, low elevation rivers where monthly averages exceed 24°C (Isaak et al. 2017).

### Hydroclimatic data sets

To obtain a dataset for describing regional AT trends, we extracted monthly records for June, July, and August at 690 stations from the Global Historical Climate Network-Monthly (GHCNM) dataset, Version 4 (Menne et al. 2018; <https://www.ncei.noaa.gov/products/global-historical-climatology-network-monthly>) that spanned the 40-year period of 1976–2015. The beginning of this period coincides with the globally coherent warming signal that emerged in the 1970s (Rahmstorf et al. 2017) and it spans enough time to temper the effects of short-term climate cycles such as the Pacific Decadal Oscillation (periodicity of 20–30 years) and El Niño–Southern Oscillation (periodicity of 2–5 years) that dampen or exacerbate seasonal patterns of precipitation and ATs in the northwestern U.S. (Mantua et al. 1997; McCabe and Dettinger 1999; Mote et al. 2003). The GHCNM data set is bias corrected and homogenized to account for station relocations or changes in instrumentation and is considered the best available long-term AT records (Lawrimore et al. 2011).

Months with missing AT values occurred for 28% of the station-year-months in the extracted data set, so the records were completed using an imputation technique performed with the MissMDA package (Missing Values

with Multivariate Data Analysis; Josse and Husson 2016) in R (R Core Team 2020). This technique uses correlations among sites in time-series records to accurately estimate missing values by first applying standard principal components analysis to the incomplete dataset where missing values have been replaced with column means. Data are then reconstructed from the principal components and the initial analysis step repeated but with missing values replaced using estimates from the reconstructed data (Josse and Husson 2012). Covariation among the monthly AT observations at the 690 stations was strong, so the average correlation between observed AT values and those predicted by the imputation technique was high ( $r = 0.96$ ). After imputation, all temperature records were complete and decadal trends in monthly temperatures at each station were calculated as the slope parameter (multiplied by 10) from simple linear regressions of AT on year for the 40-year period described above. These trend estimates were plotted against station elevation values and linear regression again used to describe potential EDW relationships.

To describe regional Q trends, monthly data for June–August were downloaded from the National Water Information System (NWIS: <https://waterdata.usgs.gov/nwis/rt>) for 131 gage sites on unregulated rivers and streams with relatively complete records from 1976 to 2015. These records were missing values for 12% of gage-year-months, which were imputed using the MissMDA package and results showed a similarly strong correlation between observed and predicted values. Decadal trends in monthly Q at each station were calculated from the slope parameter in simple linear regressions of Q on year over the 40-year period and expressed as percent change relative to average flows at the beginning of the record period. Trend estimates were plotted against gage site elevation and linear regression used to describe potential EDW relationships.

Long-term  $T_w$  records in the northwestern U.S. are relatively common for large rivers and were examined previously to reveal summer warming trends of 0.14–0.27°C/decade for the period of 1976–2015 (Isaak et al. 2018a). Comparable long-term records from headwater streams in the region are rare, however, so inference concerning warming rates in high elevation systems has been based on statistical estimates of  $T_w$  sensitivity to AT variation (Luce et al. 2014). This approach has revealed the limited sensitivity of cold, high-elevation streams (e.g.,  $< 0.5 \text{ } ^\circ\text{C}_{T_w}/^\circ\text{C}_{AT}$ ), which is predicted to result in small  $T_w$  increases in association with long-term regional AT increases (Isaak et al. 2016). Although useful, the sensitivity approach provides indirect inference concerning EDW and has relied on  $T_w$  records

**Table 1.** Descriptive statistics of stream temperature monitoring sites used to assess elevation-dependent warming patterns in the northwestern U.S.

| Study area                           | Mean   | Median | SD     | Minimum | Maximum |
|--------------------------------------|--------|--------|--------|---------|---------|
| Rocky Mountain sites (n = 226)       |        |        |        |         |         |
| Elevation (m)                        | 1,392  | 1,407  | 464    | 280     | 2,369   |
| Drainage area (km <sup>2</sup> )     | 687    | 47.3   | 3,011  | 2.18    | 34,865  |
| Mean annual flow (m <sup>3</sup> /s) | 7.37   | 0.692  | 26.4   | 0.0253  | 281     |
| Reach slope (m/m)                    | 0.0389 | 0.0273 | 0.0403 | 0.001   | 0.150   |
| T <sub>w</sub> June (°C)             | 8.53   | 8.34   | 2.50   | 3.54    | 18.0    |
| T <sub>w</sub> July (°C)             | 12.3   | 11.9   | 2.83   | 7.24    | 20.9    |
| T <sub>w</sub> August (°C)           | 12.5   | 12.1   | 2.78   | 7.78    | 22.5    |
| Cascade Range sites (n = 45)         |        |        |        |         |         |
| Elevation (m)                        | 660    | 636    | 177    | 304     | 1,105   |
| Drainage area (km <sup>2</sup> )     | 996    | 571    | 1,168  | 18.5    | 4,284   |
| Mean annual flow (m <sup>3</sup> /s) | 13.8   | 9.21   | 15.4   | 0.112   | 50.9    |
| Reach slope (m/m)                    | 0.0258 | 0.010  | 0.0293 | 0.001   | 0.122   |
| T <sub>w</sub> June (°C)             | 9.02   | 9.18   | 1.78   | 5.53    | 15.3    |
| T <sub>w</sub> July (°C)             | 12.7   | 13.1   | 2.13   | 8.84    | 18.4    |
| T <sub>w</sub> August (°C)           | 13.5   | 13.5   | 1.84   | 10.3    | 17.9    |

obtained over different monitoring periods and lengths of time that may introduce undesirable variability. A more direct approach for assessing stream EDW involves calculating T<sub>w</sub> lapse rates across a broad elevation range using continuously recording sensors during the same multiyear period which includes contrasting hydroclimatic conditions. If positive EDW occurs, the expectation is that these gradients will weaken during warm periods when stream Q is low because high-elevation streams will warm more than low-elevation streams. If negative EDW occurs, however, an opposing pattern will manifest as these gradients strengthen and the differences between high- and low-elevation streams increase.

T<sub>w</sub>-elevation lapse rates are easily calculated and can be examined for intra-annual or inter-annual periods, although the latter is considered a better analogue for climate change scenarios because it negates the effect that changing sun angle has on stream heating dynamics (Luce et al. 2014). Concerns have been expressed that gradual warming of groundwater aquifers will enhance future sensitivity of T<sub>w</sub> to climate forcing (Kurylyk et al. 2015; Leach and Moore 2019), in which case short-term analogues based on inter-annual changes could inaccurately portray long-term dynamics. However, such concerns are most relevant to areas warmer than many mid- to high-latitude mountain ranges where winter temperatures are frequently below 0°C for multi-week or monthly periods and the inter-annual transfer of heat through shallow hillslope aquifers is unlikely. In our study area, for example, mean January AT at the monitoring stations described above are usually subzero once elevations exceed ~800 m and average -10°C at high elevation sites within the region (Supplementary information, Figure 1).

To examine T<sub>w</sub>-elevation gradients, we drew from a data set published by Isaak et al. (2018b) that consists of records at 226 sites in small streams to large

ivers which were continuously monitored from January 2011 through December 2015 across a 2,000 m elevation gradient (300 m to 2,300 m) in the Rocky Mountains of central Idaho (Table 1; Figure 1). These data were supplemented with continuous records for the same period from 45 sites along the eastern flank of the Cascade Range that were downloaded from the NorWeST database (<https://www.fs.usda.gov/rm/boise/AWAE/projects/NorWeST.html>) and ranged in elevation from 304 m to 1,105 m. In both areas, none of the T<sub>w</sub> monitoring sites were affected by reservoirs or glaciers, headwater lakes were rare, and other anthropogenic influences were limited due to the rugged topography, low human population densities, and limited development. Climatic variability during 2011–2015 was considerable and included a relatively cool year in 2011 that began with an April 1 snow-water equivalent that was 120% of the 1991–2020 median value (U.S. Department of Agriculture National Water and Climate Center: <https://www.nrcs.usda.gov/wps/portal/wcc/home/>) and translated to high flows during spring and early summer months. At the other extreme was the winter of 2014–2015, infamously known in many parts of the northwestern U.S. as the snowless winter, that was followed by anomalously low summer stream flows (Mote et al. 2016; Marlier et al. 2017). April 1 snow-water equivalent values in 2015 were 40% of the long-term median values in the Cascade Range watersheds associated with T<sub>w</sub> sites and 60% of the long-term median values in the Rocky Mountain Range subdomain. As a result, summer Q values at gages were in the lowest 5<sup>th</sup>-percentile of historical records at many gages (Mote et al. 2016; VerWey et al. 2018; NWIS), which when accompanied by anomalously warm AT translated to extreme conditions and widespread mortalities of migrating

salmon and other fish species throughout the region's rivers (Columbia Basin Bulletin 2015). Based on a 77 year  $T_w$  record from the Columbia River, temperatures were in the highest 95<sup>th</sup>-percentile during the summer of 2015 (Isaak et al. 2018a).

### Thermal habitat example

We assessed how different forms of EDW would affect the distribution and extent of cold-water habitats in a mountain river network by focusing on a 757 km network that drains a mountainous 2,180 km<sup>2</sup> basin in central Idaho. In this area, mean August  $T_w$  values were predicted at 1-km resolution for a baseline climate period of 1993–2011 from observations at 418 sites using a statistical stream-network model as part of the regional NorWeST project (Isaak et al. 2017). Hypothetical organisms that required habitats colder than the isotherms associated with 11 °C, 13 °C, or 15 °C were assumed to occupy the network, which resulted in patchy and fragmented initial distributions of thermally suitable areas that are characteristic of many headwater species. We then applied two EDW scenarios to the baseline  $T_w$  pattern wherein temperatures throughout the network were increased by an average of 1 °C but with warming gradients of either 0.1 °C/1,000 m (positive EDW) or –0.1 °C/1,000 m (negative EDW) across the 1,600 m between the lowest network reach and the highest reaches where channel slopes exceeded 15% and provide barriers to dispersal by most stream vertebrates. For the baseline and EDW scenarios, the total length of habitats < 11 °C, < 13 °C, and < 15 °C were summarized and patterns of habitat loss compared.

## Results

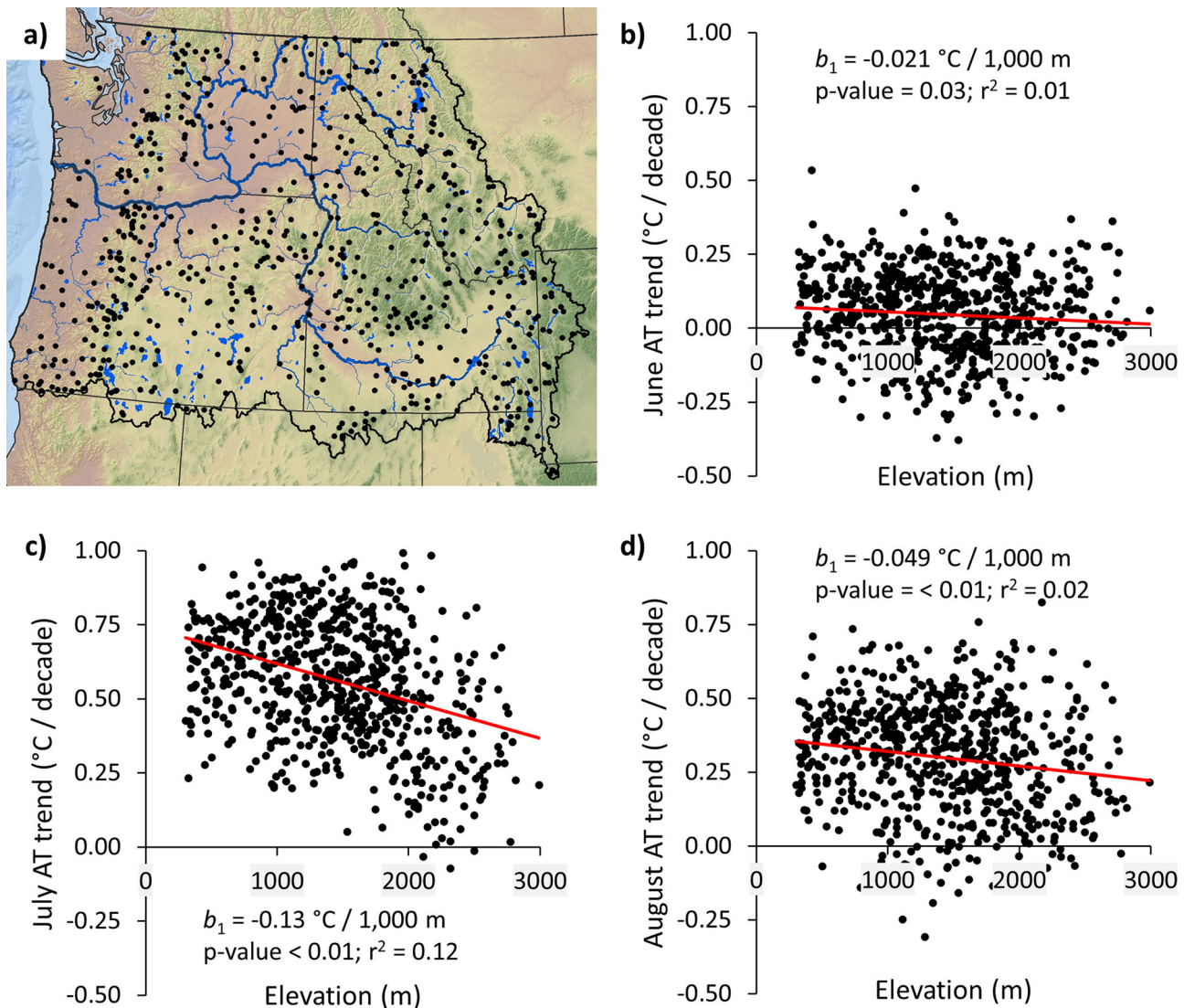
Regional warming trends occurred in the study area during the summer months of 1976–2015, as indicated by average AT trends of 0.05 °C/decade in June, 0.56 °C/decade in July, and 0.30 °C/decade in August (Figure 2; Supplementary information, Figure 2). Heterogeneity among AT stations was substantial but statistically significant EDW patterns occurred in all three months and indicated that high-elevation sites usually warmed less than low-elevation sites. Elevation dependence was also apparent in Q trends but the largest declines were observed for the highest elevation gages (Figure 3; Supplementary information, Figure 3). The differences between high and low elevation gages were most pronounced during June, which encompasses the tail-end of the snowmelt

runoff period. By August, when baseflow conditions prevailed throughout the region, the elevation gradient had weakened and the majority of gages showed long-term declining trends.

Intra-annual cycles in  $T_w$ -elevation gradients for 2013 are shown in Figure 4 and were similar for each of the five years. As expected, weak or nonexistent elevation trends manifest during cold winter months when  $T_w$  at many sites were at or near 0 °C due to exposure to sub-zero ATs. As temperatures warmed in the spring, a small  $T_w$ -elevation gradient appeared, which then steepened into the warmest summer months before beginning to flatten in the fall. At the conclusion of the annual cycle, the highest elevation streams exhibited an average range of 10–11 °C, which was less than the 16–17 °C range exhibited in the lowest streams.

More relevant with regards to possible future changes,  $T_w$ -elevation gradients based on inter-annual changes steepened during June and July between the cold high-flow year in 2011 and the warm low-flow year of 2015, thereby indicating a pattern of negative EDW (Figure 5). In the Rocky Mountain streams during June, the slope of the regression line describing the temperature gradient was –1.8 °C/1,000 m in 2011, which steepened 89% to –3.4 °C/1,000 m in 2015 as average water temperatures increased by 5.6 °C. The highest elevation streams warmed an average of 4.2 °C between these years; whereas low elevation streams warmed by 7.5 °C. These changes occurred as average June AT increased by 6.5 °C and Q decreased 78% at monitoring stations within the Rocky Mountain subdomain. Similar patterns were observed between the two extreme years during the month of July. During August when streams were at baseflows, the  $T_w$ -elevation gradients were similar (Figure 5e), although relatively little inter-annual variation occurred in AT or Q that could have resulted in elevation dependent responses. In the Cascade Range streams, a pattern of negative EDW in June and July was apparent between the two extreme climate years although the changes were smaller than in Rocky Mountain streams. During June of 2011, the  $T_w$ -elevation gradient was –7.1 °C/1,000 m, which steepened 11% to –7.9 °C/1,000 m in 2015 as AT increased by 6.7 °C and Q decreased by 74% at stations in the Cascade Range subdomain.

In the thermal habitat example, 577 km (76.2%) of the 757 km network was classified as thermally suitable at < 13 °C in the baseline condition, a number that decreased by 76 km to 501 km in the positive EDW scenario (Table 2; Figure 6). Counterintuitively, the amount of thermal habitat reduction was greater in the negative EDW scenario, involving the loss of 98 km to



**Figure 2.** Locations of 690 stations in the northwestern U.S. where air temperatures were monitored from 1976 to 2015 (a) and relationships between elevation and monthly air temperature trends during this period for June (b), July (c), and August (d). Parameter estimates describe the slope of the linear regression trend lines. Maps showing trends at individual stations are provided in [supplementary information](#).

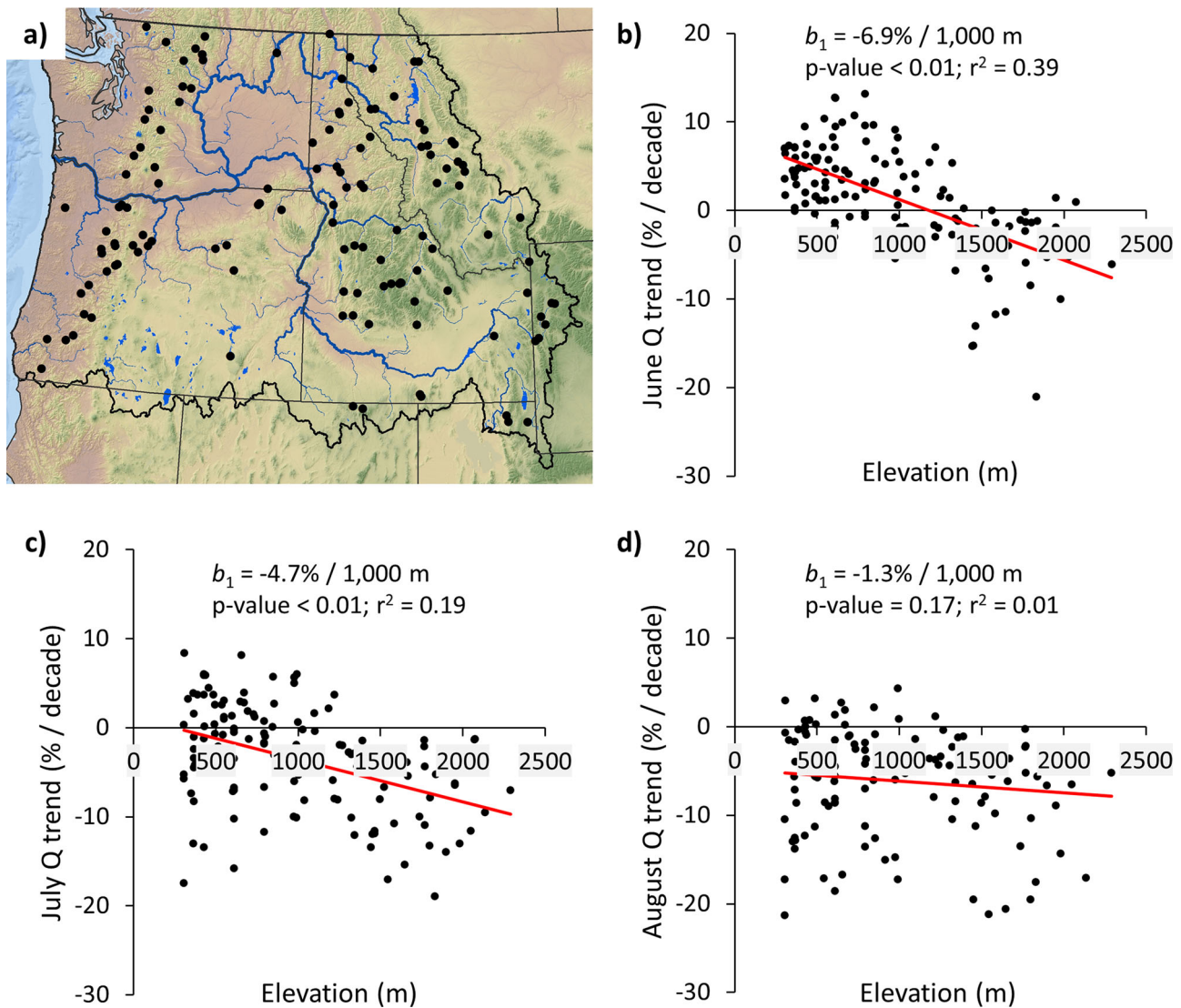
479 km of stream considered suitable. This occurred because more warming happened in downstream reaches that were close to the 13 °C threshold; whereas in the positive EDW scenario more warming occurred where  $T_w$  was well below the temperature threshold and these reaches remained thermally suitable. Despite these differences, however, the areas where habitats became unsuitably warm and the distributions of remaining habitats were similar between the two forms of EDW (Figure 6, panels d and e). In both cases, the coldest waters and suitable habitats remained spread through upper portions of the network, unsuitably warm areas occurred downstream, and areas of habitat loss were intermediate between the two extremes. Results based on the 11 °C and 15 °C isotherms also indicated greater habitat losses associated with the

negative EDW scenario (Table 2), although the loss differences between the types of EDW scenarios were negligible for the 11 °C isotherm which restricted thermal habitats to only the steepest headwater reaches. The key insight from this example was that only small portions of the overall habitat losses were due to positive or negative EDW, and the majority losses were associated with the mean  $T_w$  increase of 1 °C throughout the network.

## Discussion

### Elevation dependent stream patterns

Despite rapid climate change in recent decades, our results suggest that negative EDW of streams has been

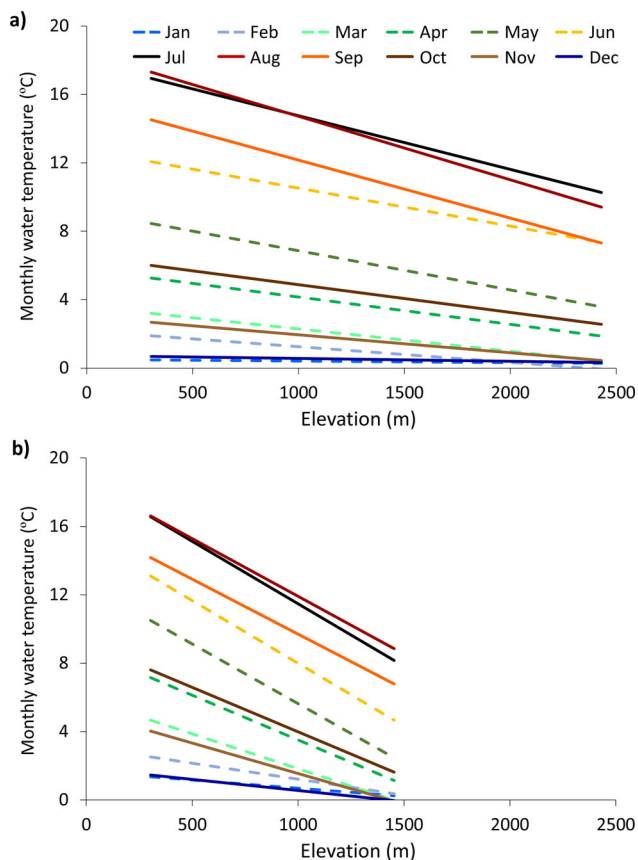


**Figure 3.** Locations of 131 gages on unregulated streams and rivers in the northwestern U.S. where discharge was monitored from 1976 to 2015 (a) and relationships between elevation and monthly discharge trends during this period for June (b), July (c), and August (d). Parameter estimates describe slopes of the linear regression trend lines. Maps showing trends at individual stations are provided in [supplementary information](#).

the historical pattern in the northwestern U.S. Effects of elevation-dependent trends in AT and Q that act as long-term climate forcings have been countervailing with regards to  $T_w$ , which has probably allowed advective cooling of high-elevation streams from massive seasonal snowmelt contributions to dominate elevation-dependent responses (Yan et al. 2021; Siegel et al. 2022). Added support for negative stream EDW is provided by the inter-annual responses observed in both Cascade Range and Rocky Mountain streams to the strong contrasts in climatic conditions between the extreme years of 2011 and 2015. Although ongoing reductions in snowpack are expected to reduce the advective cooling effect on the region's streams, many high-elevation basins, especially within the Rocky Mountains, are predicted to remain cold enough to

accumulate sizeable winter snowpacks despite continued warming through at least the end of the century (Lute and Luce 2017; Ikeda et al. 2021). In fact, based on recent historical winter AT warming rates of 0.3–0.4 °C/decade (Abatzoglou et al. 2014; Isaak et al. 2018a), each 1 °C increase will require two or three decades to occur and many high-elevation basins could retain seasonal snowpacks into the late 22<sup>nd</sup> century. Over such a long time-horizon, warming rates could change and acceleration would mean faster snowpack losses but evidence has yet to emerge that this is occurring (Rahmstorf et al. 2017) and it could also be the case that future warming rates decrease as greenhouse gas emissions are reduced.

Despite these results, it is unclear how representative the stream responses observed in the



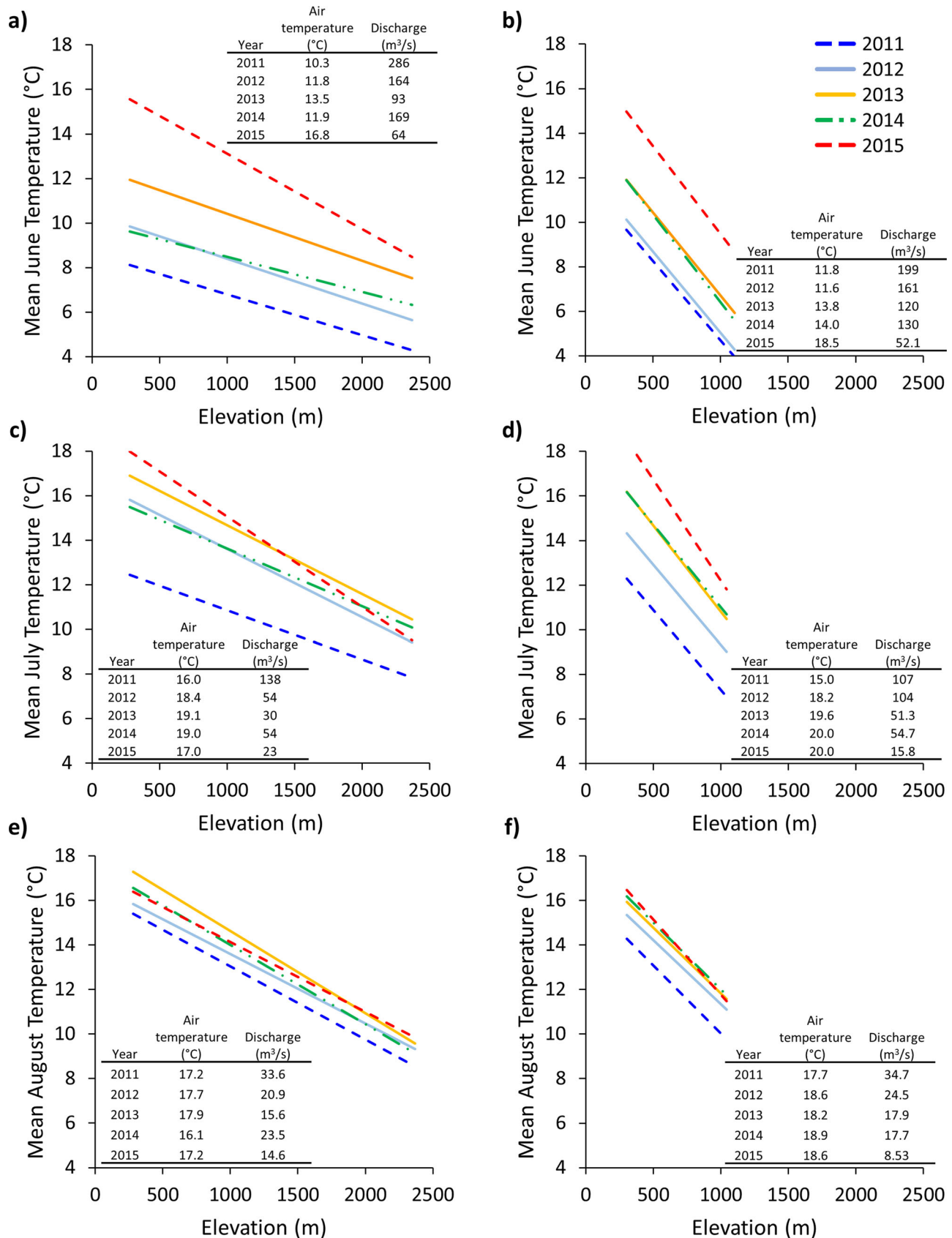
**Figure 4.** Linear regression trend lines describing intra-annual water temperature-elevation relationships in 2013 observed at continuously monitored sites in streams across a portion of the Rocky Mountains (panel a) and the Cascade Range (panel b). Data values are hidden to improve visibility of trend lines.

northwestern U.S. may be of other mountainous regions. Because mountain ranges often exhibit enhanced elevation warming of AT (MRI 2015; Pepin et al. 2022), in some locales this trend could work in concert with Q decreases to effect larger thermal gains in high elevation streams. However, we are unaware of case histories which have thus far documented positive stream EDW, and where  $T_w$  monitoring networks have been established across elevation transects, the opposing pattern usually occurs. For example, steep high-elevation streams draining a coastal area in western Alaska were estimated to be 5–8 times less sensitive to summer AT variation than lower elevation sites (Lisi et al. 2015) and this reduced sensitivity gradient persisted in warm years with little snowpack during the preceding winter (Cline et al. 2020). In the Swiss Alps, Piccolroaz et al. (2019) observed that the smallest temperature increases during European heat waves were in high-elevation streams with hydrologic cycles dominated by snowmelt inputs. Also in the Alps, Michel et al. (2020) described trends over a 50-year period and found that high-elevation streams

had warmed about half as much as low-elevation streams. Results from both regions come with caveats, however, due to the influences of glaciers on some streams and in the case of Switzerland, water development projects that could affect patterns of warming. Although thermal patterns in streams draining tropical mountain ranges have been less studied, descriptions of  $T_w$ -elevation relationships from these systems might be particularly interesting due to an absence of snow-related cooling effects and perhaps stronger precipitation gradients between high- and low-elevations. Regardless, the ease with which stream temperatures can be monitored using inexpensive sensors, growing  $T_w$  and hydroclimatic databases that can be mined for information, and the relevance of the question to forecasting and potential model revisions should encourage efforts to develop additional case studies and broader comparisons that may reveal different responses.

An unexpected result from the thermal habitat example was that the form of stream EDW had a minor effect on the amount and distribution of habitat loss compared to the average magnitude of temperature gain throughout a river network. In retrospect, however, this is sensible for mountain river networks where pronounced longitudinal  $T_w$  gradients mean that headwater reaches are often far below a temperature threshold and the small additional amounts of warming associated with elevation dependency are consequential only where initial conditions approach the threshold. Although the habitat example could be viewed as ecologically simplistic, thermal thresholds strongly correlate with community structure and species distributions in aquatic ectotherms (Parkinson et al. 2016; Mandeville et al. 2019) and the example accurately portrays how species distribution models are frequently used to predict suitable habitat areas in climate vulnerability assessments (Elith et al. 2009; Isaak et al. 2015). The stability of thermal habitat distributions, regardless of the EDW pattern, provides some margin for error in  $T_w$  forecasts and leads us to conclude that accelerated losses of headwater climate refugia on the basis of positive EDW are likely to prove overly pessimistic (Steel et al. 2019; Cline et al. 2020).

More concerning with regards to elevation dependency were the summer Q declines that disproportionately affected headwater areas relative to lower elevation streams. Decreasing winter westerly wind speeds that weaken orographic effects have likely enhanced this pattern within the northwestern U.S. (Luce et al. 2013; Kormos et al. 2016) but forecasts



**Figure 5.** Linear regression trend lines describing inter-annual variation in water temperature-elevation relationships in 2011–2015 for June, July, and August observed at continuously monitored sites in streams across a portion of the Rocky Mountains (panels a, c, and e; data values are hidden to improve visibility of trend lines) and the Cascade Range (panels b, d, and f). Inset tables provide values of mean monthly air temperatures and stream discharge that were measured at monitoring stations across the study areas during the same periods.

**Table 2.** Extent of thermally suitable habitat associated with different isotherms, forms of elevation-dependent warming, and a 1°C temperature increase across the mountain river network shown in Figure 6.

| Isotherm | Baseline | 1 °C warming scenario |              |             |
|----------|----------|-----------------------|--------------|-------------|
|          |          | Positive EDW          | Negative EDW | Neutral EDW |
| 11 °C    | 389 km   | 280 km                | 278 km       | 279 km      |
| 13 °C    | 577 km   | 501 km                | 479 km       | 490 km      |
| 15 °C    | 685 km   | 653 km                | 630 km       | 638 km      |

driven only by warming and lost snowpack also predict that declines in summer low flows will continue (e.g., Wu et al. 2012; Vano et al. 2015). Ongoing reductions are likely to have important biological consequences by confining organisms to smaller habitat volumes, enhancing competitive interactions, and reducing flow velocities and oxygen availability, all of which may deleteriously affect growth and potentially survival (Harvey et al. 2006; Birrell et al. 2020; Jacobsen 2020). Within the smallest headwater streams, reductions could also increase the incidence and spatial extent of flow intermittency to incur direct mortality of organisms within the affected reaches (Datry et al. 2014). As a consequence, future bioclimatic assessments for mountain headwater fauna should expand beyond the temperature-centric approach that has been most common (Comte et al. 2013) to also account for trends in streamflow and address risks more comprehensively (e.g., Isaak et al. 2022; Tonina et al. 2022).

### *T<sub>w</sub> model forecast discrepancies*

#### *Groundwater assumptions*

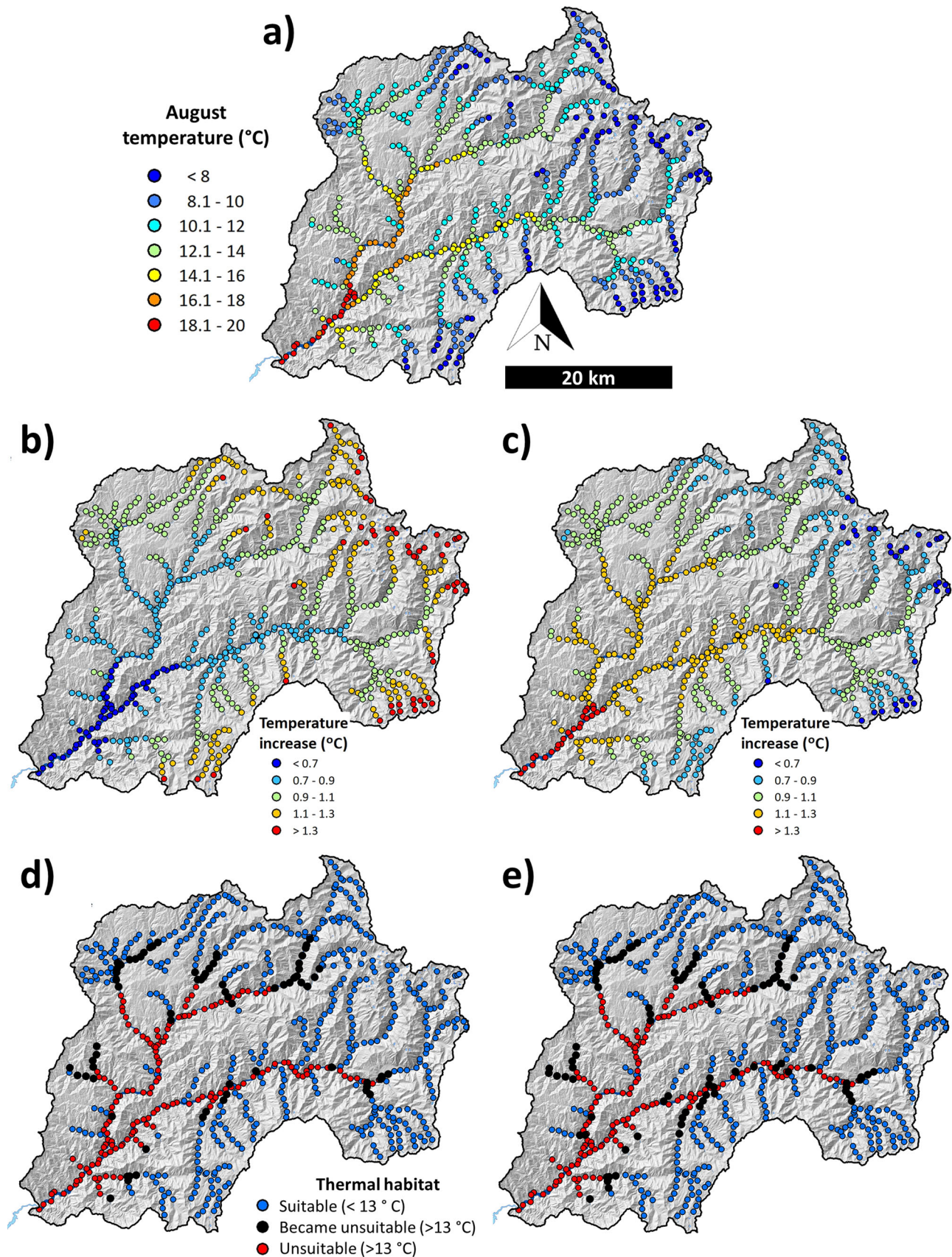
The important question remains, why do statistical and mechanistic  $T_w$  models forecast differences in stream EDW? The general framing of the issue from the perspective of the mechanistic modeling literature is that many statistical models rely on sensitivity measured at short time scales, so that extrapolation to the effects of large temperature changes over the course of decades does not include the warming of groundwater that sets the upstream boundary conditions for headwater streams (Kurylyk et al. 2015; Leach and Moore 2019; Yan et al. 2021). As noted earlier and shown in the [Supplementary Information](#), however, mid-winter AT in many mountain environments are so far below 0°C that the inter-annual transfer of heat which would gradually increase groundwater temperatures appears unlikely in many headwater basins for all but the most extreme climate change scenarios. Moreover, when the mechanistic models are examined, this groundwater effect is

usually modeled by setting the groundwater temperature to the mean annual air temperature (Cristea and Burges 2010; Wu et al. 2012; Ficklin et al. 2014; Leach and Moore 2019; Yan et al. 2021), which is justified from groundwater textbooks (e.g., Mazor 2003). This generates a pattern that nominally follows steady state expectations associated with heat conduction into the ground, but it “equilibrates” the effects of those boundary conditions much more rapidly than would be theoretically expected (e.g., Kurylyk et al. 2015; Burns et al. 2017). Beyond this, and more importantly, the equivalence of mean annual temperature and groundwater temperature is known to be approximate at best, and generally incorrect in mountain basins, where snowmelt water inputs and permafrost cause departure from such a relationship (Manning and Solomon 2003, Burns et al. 2017; Kury et al. 2017), and departure from the implied thermal sensitivity (Kurylyk et al. 2013).

The upshot is that mechanistic models have code that specifies a sensitivity of  $\sim 1.0\text{ }^{\circ}\text{C}_{\text{Tw}}/^{\circ}\text{C}_{\text{AT}}$  in contrast to the lower empirical estimates often observed in the uppermost network segments ( $< 0.5\text{ }^{\circ}\text{C}_{\text{Tw}}/^{\circ}\text{C}_{\text{AT}}$ ). This is expected to be an overestimate based on physical reasoning, but because the energy balance in mechanistic models moderates change estimates in downstream segments, a positive EDW may result. Thus, the imposition of a specified upstream temperature boundary condition essentially sets the sensitivity of headwater segments where energy balances between stream and atmosphere have less opportunity to play out. Modelers need to be cognizant that this represents a potential consequence of boundary condition choices rather than an emergent result of calculated shifts in energy and mass balances in the models. The important point is that many mechanistic models, as currently constructed, cannot confirm the hypothesis that long term  $T_w$  sensitivities are substantially greater than those estimated from statistical approaches. Rather, they illustrate the consequences IF they were. This means there is still a need for empirical evaluations of the proposition and additional analysis of long-term records will be necessary to adequately understand the effects of long duration air temperature increases on headwater stream temperatures.

#### *Linkages between $T_w$ and climate models*

Differences in EDW predictions could also arise from how  $T_w$  models use the AT and precipitation outputs from GCMs. However, although future AT deltas are important drivers of prediction forecasts from  $T_w$  models, they are an unlikely source of these



**Figure 6.** Effects of contrasting patterns in elevation dependent stream warming on  $T_w$  and distributions of thermally suitable habitat for a hypothetical organism which requires temperatures  $< 13^\circ\text{C}$ . Panel a shows the mean August  $T_w$  values that were interpolated from observations at 418 unique sites within the network. Subsequent panels show future deltas which averaged temperature increases of  $1^\circ\text{C}$  but with positive elevation-dependent warming (panel b) or negative elevation-dependent warming (panel c). Panels d and e show distributions of reaches  $< 13^\circ\text{C}$  after adding temperature values in panels a and b or panels a and c.

differences because grid cell sizes of GCMs have horizontal resolutions of 100–300 km (i.e., 10,000–90,000 km<sup>2</sup>; Mote and Salathé 2010; Maurer et al. 2014) and are too coarse to represent elevation dependency in mountainous terrain. Moreover, this coarseness means that the same  $T_w$  delta values are often used to force  $T_w$  models across broad areas. Precipitation is the other main output from CGMs, which is usually translated to stream Q scenarios via distributed hydrologic models (e.g., Liang et al. 1994; Wigmosta et al. 1994) prior to its use in  $T_w$  model forecasts. Similar to the historical pattern observed in the northwestern U.S., these Q scenarios predict the largest summer flow declines will occur in high-elevation streams (Wu et al. 2012; Vano et al. 2015; Yan et al. 2021). In mechanistic models, these different Q delta values then inform site-specific calibrations associated with available  $T_w$  records and temperature increases are predicted accordingly. Enhancing the pattern of positive elevation dependency that may result, some mechanistic  $T_w$  models could be overly sensitive to changes in Q. Wu et al. (2012) acknowledged this possibility, as their model sensitivity analysis suggested that a 20% Q decline caused a 0.96 °C  $T_w$ , similar in magnitude to the 1.25 °C  $T_w$  increase that was expected from a 2 °C AT increase. These results contrast with empirical estimates from stream sites with multidecadal records in the same region that indicate 80–90% of historical  $T_w$  increases are attributable to trends in AT rather than Q (Isaak et al. 2012). Similar patterns are commonly reported from other regions where the preponderance of long-term  $T_w$  gains are linked most strongly to AT increases (Webb and Nobilis 2007; Markovic et al. 2013; Arora, Tockner, and Venohr 2016; Chen et al. 2016; Michel et al. 2020).

In contrast to mechanistic  $T_w$  models, the statistical approaches thus far applied to river network  $T_w$  forecasts (Isaak et al. 2017; Jackson et al. 2018; FitzGerald et al. 2021) do not use Q scenario information from hydrologic models in a distributed fashion and therefore cannot recognize elevation dependency in flow forecasts. Instead, an average Q delta between historical baseline and future climate periods is calculated for the stream sites within a network model domain and is multiplied by a Q parameter in the  $T_w$  model to estimate a future temperature change. The effects of historical and future AT variability are addressed in a similar manner. Therefore, forecasts which exhibit negative stream EDW, as do those in the northwestern U.S. from the model developed by Isaak et al. (2017), do so because the historical data sets

used in model development manifest this pattern. A limitation of this statistical approach is an inability to accommodate a weakening or reversal in the pattern of elevation dependency should it occur in the future. However, spatio-temporal statistical models for stream networks have recently been developed which could be configured to account for this dynamic process but these have yet to be applied at network scales for  $T_w$  forecasting and remain computationally intensive (Santos-Fernandez et al. 2022).

### *Extrapolating in space and time*

Additional factors relevant to elevation dependency in  $T_w$  predictions are issues associated with model calibration and the inferential domains to which models are applied. The use of statistical models in forecasting has been cautioned against (Arismendi et al. 2014; Leach and Moore 2019) and generally speaking, we agree that extrapolating beyond the range of climatic variation encompassed by a statistical  $T_w$  model creates additional uncertainty. However, this uncertainty should be contextualized based on the amount of extrapolation relative to the variability encompassed by data sets used in model development. In many areas where  $T_w$  data sets are common, they may already encompass a wide range of climatic variability and extreme years often represent what are projected to be average conditions in future climate scenarios such that minimal extrapolation is required. Less discussed but conceptually similar to temporal extrapolation is spatial extrapolation beyond the locations where  $T_w$  observations occur to generate network-scale prediction scenarios. River networks are expansive landscape features that encompass hundreds to tens of thousands of kilometers and their sheer size and range of conditions remain underappreciated (Bishop et al. 2008). Across these large extents, both statistical and mechanistic models may be vulnerable to spatial prediction bias if calibrated or fit to a non-representative sample of conditions and then applied outside these conditions.

One factor potentially causing bias in statistical model predictions is spatial autocorrelation which arises from non-independence among samples. This phenomenon is common in large datasets that often encompass hundreds to thousands of  $T_w$  sites and exhibit high degrees of spatial clustering that over-represent conditions in portions of networks (Isaak et al. 2014). For this reason, we have gravitated to the use of spatial-statistical network models that explicitly address this nonindependence by using an autoregressive error term to yield unbiased parameter estimates

(Ver Hoef et al. 2006; Rushworth et al. 2015). Despite this, we have also encountered instances when predictions of summer temperatures in headwater channels were substantially less than 0 °C, which is physically impossible. Examination of these sites revealed them to be in especially steep, distal portions of drainage networks where channel slopes consistently exceeded 20%, and which were beyond the range of stream conditions sampled with temperature sensors. The remedy was to constrain model predictions to less steep portions of the network where the  $T_w$  model was empirically supported and inference was reliable.

Mechanistic models, by virtue of more intensive data requirements, are frequently calibrated to a small number of sites, e.g., 5–50, within river networks. This alone is not problematic if the sites are representative of network conditions and any distinctions that may occur in physical process domains. However, it is usually the case that calibration occurs to  $T_w$  sites on larger rivers at low elevations because these often have co-located Q gages and other hydrometeorological sensors which are useful for heat budget calculations. Distributions of Q gages globally are known for this spatial bias (Krabbenhof et al. 2022) and it is also true within the northwestern U.S. where mechanistic  $T_w$  models used in regional projections have been calibrated to a small number of sites on large rivers (Wu et al. 2012; Ficklin et al. 2014). As a result,  $T_w$  predictions in headwater areas must rely on assumptions about the constancy of physical process interactions and the accuracy of methods used to represent these processes for heat budget calculations throughout the network (Benyahya et al. 2010; Lute and Luce 2017).

#### **Future $T_w$ research**

Given the preceding discussion, several avenues of research seem relevant to improving future  $T_w$  models and resolving uncertainties about how thermal regimes will evolve in mountain landscapes. Most fundamentally, both statistical and mechanistic models could benefit from advances in complementary fields that enable better representations of key covariates and physical processes at broad scales. Rather than reliance on coarse AT outputs from GCMs, for example,  $T_w$  models could instead use downscaled regional climate models with higher grid cell resolutions that are capable of representing elevation dependency (Palazza et al. 2019). These models could be further downscaled using topo-climate models with resolutions as fine as 1 km<sup>2</sup> in some instances (Daly et al. 2008; Oyler et al. 2015). At these

resolutions, additional microclimatic phenomenon that are common to mountain environments such as cold-air drainage or the differences in AT variability between valley bottoms, hillslopes, and ridgelines might also be resolved (Daly et al. 2010; Holden et al. 2016). Decouplings between macroclimatic models and microclimatic realities in mountainous terrain have thus far been ignored in  $T_w$  model development and forecasting but have the potential to create systematic biases because GCMs simulate conditions associated with freely circulating air masses above terrain influences where long-term temperature increases may differ from those which occur in valleys (Pepin and Seidel 2005; Daly et al. 2010). Additional remote sensing data products from satellite platforms offer comprehensive regional coverage and continue to improve in resolution for  $T_w$  relevant factors like vegetation characteristics and natural disturbances such as wildfire and drought (Dauwalter et al. 2017; Huylenbroeck et al. 2020). More detailed information about near-stream riparian vegetation and potential shade may be particularly relevant to future stream thermal regimes given the dominant influence of short-wave radiation in heat budgets and growing wildfire extents that are interacting more frequently with stream channels in western North America (Alizadeh et al. 2021; Ball et al. 2021).

Recent demonstrations of the importance of advective cooling from snowmelt in mountain basins (Leach and Moore 2017; Yan et al. 2021; Siegel et al. 2022) and the geographic disparities in snowpack losses that are likely to emerge this century highlight the need for this factor to be better represented in  $T_w$  models. Here again, new high-resolution data sets that portray monthly precipitation, snowfall, and snowpack at a 4-km grid resolution in North American mountain ranges have become available and could benefit future  $T_w$  models (Broxton et al. 2019; Ikeda et al. 2022). These could be applied to provide two potential improvements: 1) better estimates of how snow cover affects summer temperatures in headwater streams and 2) improved information on temporal changes in snow cover and precipitation. For example, the effect of snowfall shifting to rainfall has sometimes been framed or modeled in a way that there is an amplification of the effect of AT on hillslope and groundwater recharge temperatures (e.g. Burns et al. 2017). While the shifted timing of snowmelt versus rain during late winter can lead to lower flows with warmer temperatures during spring months because the snowmelt pulse in spring is replaced by fewer and warmer spring rains (Leach

and Moore 2019), the effect of reduced snowpack on groundwater recharge temperatures, and ultimately groundwater temperature and late season headwater channel changes, has not been explicitly addressed. Mechanistic  $T_w$  models typically assign groundwater temperatures in headwaters, and the groundwater temperature evolution models (Burns et al. 2017, Kurylyk et al. 2015) that have been used to inform  $T_w$  models usually assign recharge temperatures. From the simple perspective of bulk recharge temperature, however, snowpacks should be a buffering influence on future changes. In a simple basin where the wet-season AT is  $-2^{\circ}\text{C}$ , for example, the precipitation would fall as snow and melt releasing  $0^{\circ}\text{C}$  recharge. In the circumstance of  $3^{\circ}\text{C}$  AT warming, the precipitation would now fall (and recharge) as rain at  $1^{\circ}\text{C}$ , which represents a substantial muting compared to the overall AT warming. Between the recharge temperature and the discharge-to-headwaters temperature lay a range of conceptualizations and models about how quickly the recharged water equilibrates with atmospheric temperatures, in shallow vs. deep aquifers, and how long the water takes to reach the channel (contrast e.g. Burns et al. 2017; Kurylyk et al. 2013, 2015; Leach and Moore 2019), which depend on catchment details. Being clear on what the influence of recharge temperature change versus the influence of interflow or groundwater warming on projected changes in headwater areas would help identify remaining uncertainties on expected  $T_w$  sensitivities.

Because of the contrasting strengths and weaknesses of statistical and mechanistic models, identifying means of their constructive integration may also be useful (Dugdale et al. 2017; Slater et al. 2023). This has long occurred informally as statistical  $T_w$  modelers rely on mechanistic models for insights about key physical processes when choosing covariate proxies. As the ability to develop and apply statistical models at large spatial scales has become routine in recent years, however, more direct linkages and hybrid modeling approaches have become possible. For example, mechanistic model boundary condition inputs such as the  $T_w$  flowing into the uppermost reaches in a network could be derived from a statistical model with a spatial domain that encompassed the mechanistic model in a nested modeling structure, rather than relying on mean annual AT approximations. One challenge to establishing this linkage is the inconsistent time steps at which models are often run. Mechanistic models are usually implemented at daily time steps

and make predictions for full annual cycles whereas statistical models are more frequently run at longer weekly and monthly time-steps for the warmest summer months. However, the latter is more a reflection of the need for thermal information to predict ecological attributes such as species distributions and abundances at broad spatial scales rather than any inherent limitation of statistical models. There is no reason, therefore, that statistic models with daily time-steps or those encompassing annual cycles could not be developed as recent network-scale examples demonstrate (Jackson et al. 2018; Fitzgerald et al. 2021). Alternatively, mechanistic models could be run at courser timesteps without the loss of relevant information for many ecological applications, which would have the benefits of decreasing computational requirements and simpler formulations.

Another challenge to this hybridization is that the effects of long-duration increases in AT on  $T_w$  may not be well represented, as discussed earlier. This highlights a need to examine long-term, multidecadal  $T_w$  records to determine whether the sensitivity of streams to climate forcing is changing in ways that may lead to forecast bias as argued by Leach and Moore (2019), and if so, whether this bias is large enough to significantly degrade the utility of forecasts. Although still rare, an increasing number of multidecadal  $T_w$  records appear in the literature and could be assessed for evidence of changing sensitivities (Morrison et al. 2002; Moatar and Gailhard 2006; Lammers et al. 2007; Webb and Nobilis 2007; Kaushal et al. 2010; Isaak et al. 2012, 2018a; Orr et al. 2014; Arora, Tockner, and Venohr 2016; Chen et al. 2016; Marszelewski and Pius 2016; Michel et al. 2020; Worrall et al. 2022). Ideally for insight to mountain river networks, long-term records would be examined across a large elevation gradient within the same region but such data sets may be rare outside the Swiss Alps (Michel et al. 2020). Therefore, sensitivity estimates derived from short-term  $T_w$  records will also remain useful but more work is needed to establish the comparability of estimates derived from short- and long-term records. The advantage of the former is much larger sample sizes that potentially include hundreds of sites in many river networks. This availability enables descriptions of environmental conditions that affect  $T_w$  sensitivity (Kelleher et al. 2012; Lisi et al. 2015) and novel predictive applications wherein sensitivity patterns are mapped throughout networks to provide important landscape context (Beaufort et al. 2020).

## Conclusions

We present evidence that negative EDW has been the historical pattern in the northwestern U.S. during warm summer months, but it is unclear whether this pattern will persist and available  $T_w$  models make divergent predictions in this regard. As snowpacks within this region decline, it seems likely that the strength of advective cooling effects which have buffered many high-elevation streams will diminish in some locations and sensitivities to climate forcing will increase. However,  $T_w$  responses are also likely to vary sub-regionally depending on local elevation relief, the degree to which snowpacks are retained in high-elevation basins, and interactions among numerous factors (e.g., AT microclimates, groundwater, changes in riparian vegetation) that affect heat budget dynamics in complex mountainous terrain. Although mechanistic and statistical  $T_w$  models for river networks have advanced significantly in their accuracy, incorporation of process, and scale of application over the last decade, work remains to address important areas of uncertainty and refine forecast skill. Because of the complexities involved, modelers from both camps will benefit from collaborations going forward so that their perspectives and learnings are incorporated to the next generation of network  $T_w$  models. The increasing availability of  $T_w$  records, combined with enhanced computational capacity and the ability to better represent physical processes and landscape conditions that are relevant to thermal dynamics in river networks provide the necessary building blocks for continued advances in this important area of stream research.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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