

Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity

Daniel J. Isaak^{a,1}, Michael K. Young^b, Charles H. Luce^a, Steven W. Hostetler^c, Seth J. Wenger^d, Erin E. Peterson^e, Jay M. Ver Hoef^f, Matthew C. Groce^a, Dona L. Horan^a, and David E. Nagel^g

^aUS Forest Service Rocky Mountain Research Station, Boise, ID 83702; ^bUS Forest Service Rocky Mountain Research Station, Missoula, MT 59801; ^cUS Geological Survey, Corvallis, OR 97331; ^dUniversity of Georgia River Basins Center, Athens, GA 30602; ^eAustralian Research Council Centre of Excellence for Mathematical and Statistical Frontiers and the Institute for Future Environments, Queensland University of Technology, Brisbane, QLD 4000, Australia; and ^fNational Oceanic and Atmospheric Administration-National Marine Fisheries Service, Alaska Fisheries Science Center, National Marine Mammal Laboratory, Seattle, WA 98112

Edited by Mary E. Power, University of California, Berkeley, CA, and approved March 7, 2016 (received for review November 12, 2015)

The imminent demise of montane species is a recurrent theme in the climate change literature, particularly for aquatic species that are constrained to networks and elevational rather than latitudinal retreat as temperatures increase. Predictions of widespread species losses, however, have yet to be fulfilled despite decades of climate change, suggesting that trends are much weaker than anticipated and may be too subtle for detection given the widespread use of sparse water temperature datasets or imprecise surrogates like elevation and air temperature. Through application of large water-temperature databases evaluated for sensitivity to historical air-temperature variability and computationally interpolated to provide high-resolution thermal habitat information for a 222,000-km network, we estimate a less dire thermal plight for cold-water species within mountains of the northwestern United States. Stream warming rates and climate velocities were both relatively low for 1968–2011 (average warming rate = 0.101 °C/decade; median velocity = 1.07 km/decade) when air temperatures warmed at 0.21 °C/decade. Many cold-water vertebrate species occurred in a subset of the network characterized by low climate velocities, and three native species of conservation concern occurred in extremely cold, slow velocity environments (0.33–0.48 km/decade). Examination of aggressive warming scenarios indicated that although network climate velocities could increase, they remain low in headwaters because of strong local temperature gradients associated with topographic controls. Better information about changing hydrology and disturbance regimes is needed to complement these results, but rather than being climatic cul-de-sacs, many mountain streams appear poised to be redoubts for cold-water biodiversity this century.

climate refugia | climate velocity | biodiversity | fish | network

Mountain landscapes constitute 12% of the Earth's land surface (1) and have long served as sanctuaries for certain species by restricting human incursions and juxtaposing diverse environments (2). Mountains also host a suite of endemic species, many of which are perceived to be condemned to extinction as their habitats contract or disappear as a result of climate change-related temperature increases, environmental stochasticity, and nonnative species invasions (3–5). A substantial literature, to which we have contributed, has developed in previous decades suggesting a similar fate for cold-water fishes and other aquatic taxa in montane environments (6–8), but it rests largely on predictions about temperature increases and untested assumptions about the relationship between air temperature and water temperature. In particular, previous studies have failed to recognize that the highest and coldest streams are relatively insensitive to air temperature fluctuations (9, 10), and that the morphologies of many mountain ranges and their stream networks may mediate climate warming such that shifts in thermal habitat are small (2, 11).

Dense stream networks drain mountainous regions because of orographic enhancement of precipitation (12), and these

networks host cold-adapted species of fish, amphibians, and macroinvertebrates. Life in mountain streams (where mean annual temperatures <5 °C are common) requires special physiological adaptations (13), so aquatic communities typically have low species richness (14, 15). However, those extreme conditions also make mountain streams resistant to nonnative species invasions such that many indigenous communities remain intact even after a century of climate change and the global pandemic of anthropogenic species introductions (16). As a result, a common pattern is that warmer, low-elevation stream communities are broadly and repeatedly invaded (14, 17) whereas colder, high-elevation streams are less altered and often serve as refugia for native species tolerant of cold temperatures (18, 19). The same is true regarding more subtle genetic invasions and introgressive hybridization, because many genetically pure populations exist in headwater streams where climatic conditions limit the upstream expansion of hybrid zones (20, 21).

The ubiquity of isolated populations of many species in mountain headwaters (14, 18, 19) suggests they have existed for extended periods, but climate-induced stream warming (22, 23) raises legitimate concerns about their future persistence. Concerns are heightened by evidence of faster air temperature increases at high elevations (24), and by model predictions that streams in snowmelt-dominated landscapes will be highly sensitive (i.e., large stream $\Delta^{\circ}\text{C}/\text{air } \Delta^{\circ}\text{C}$) to air temperature increases (25–27). Such predictions, however, are at odds with recent observations from extensive monitoring networks that indicate cold streams are often the least sensitive to air temperature fluctuations (9, 10). Regardless of the stream temperature trends that are realized, their biological relevance is limited until translated

Significance

Many studies predict climate change will cause widespread extinctions of flora and fauna in mountain environments because of temperature increases, enhanced environmental variability, and invasions by nonnative species. Cold-water organisms are thought to be at particularly high risk, but most predictions are based on small datasets and imprecise surrogates for water temperature trends. Using large stream temperature and biological databases, we show that thermal habitat in mountain streams is highly resistant to temperature increases and that many populations of cold-water species exist where they are well-buffered from climate change. As a result, there is hope that many native species dependent on cold water can persist this century and mountain landscapes will play an important role in that preservation.

Author contributions: D.J.I. and M.K.Y. designed research; D.J.I., C.H.L., S.W.H., S.J.W., E.E.P., J.M.V.H., M.C.G., D.L.H., and D.E.N. performed research; D.J.I., C.H.L., S.W.H., and S.J.W. analyzed data; and D.J.I., M.K.Y., and C.H.L. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. Email: disaak@fs.fed.us.

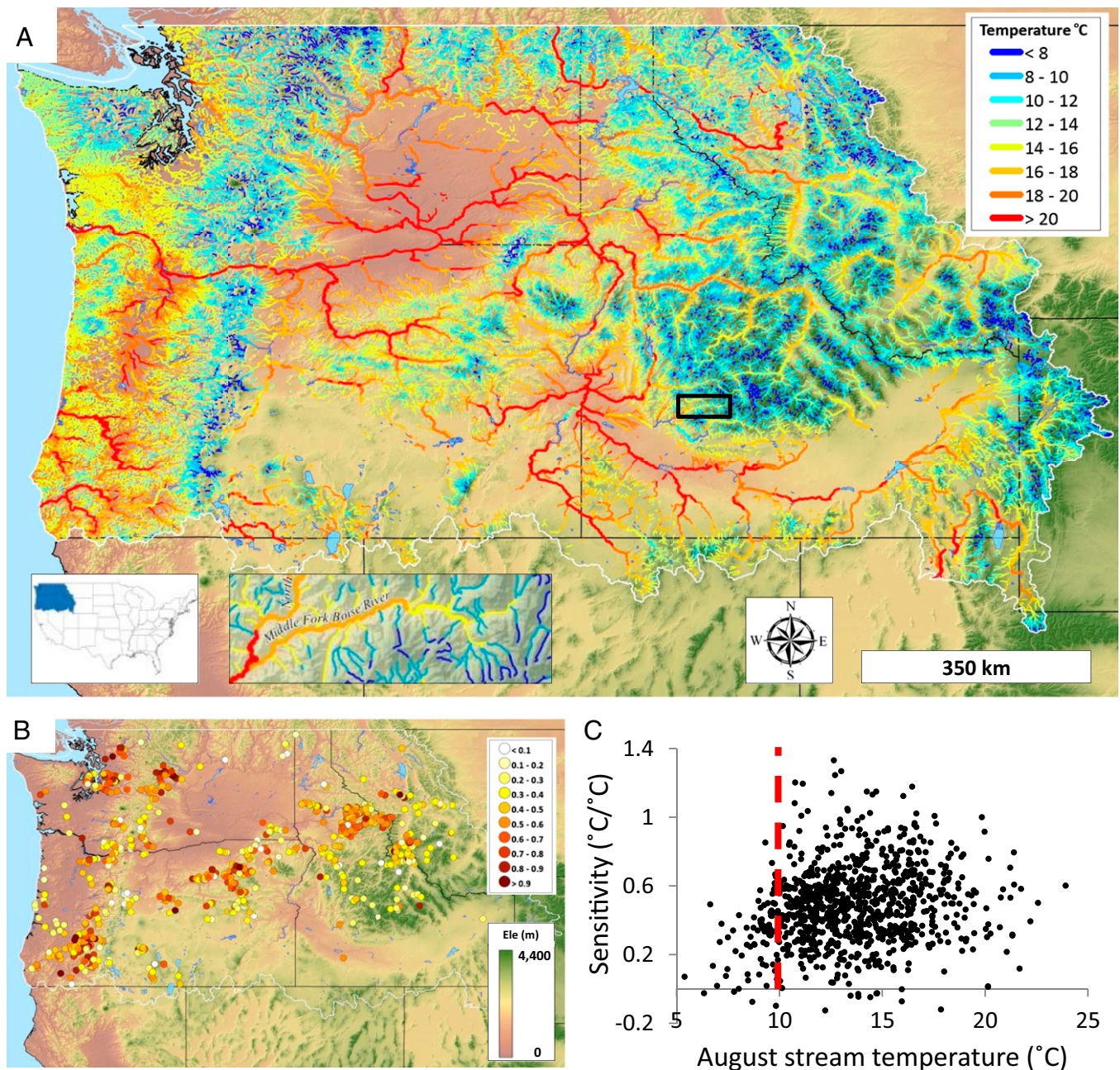


Fig. 1. August mean temperature scenario for the 222,000-km network draining the mountainous northwestern United States that was interpolated from data at 16,388 sites (*A*; *Inset* shows 1-km resolution of temperature predictions). Subset of 923 sites with long-term monitoring records where stream temperature sensitivity parameters (stream $\Delta^{\circ}\text{C}/\text{air } \Delta^{\circ}\text{C}$) were estimated (*B*; sites are color-coded by sensitivity parameter values). Relationship between sensitivity estimates and August mean stream temperatures (*C*; dashed line indicates 10 $^{\circ}\text{C}$ threshold below which sensitivity values averaged 0.32 $^{\circ}\text{C}/^{\circ}\text{C}$).

into local climate velocities (11) because these are the rates at which species distributions must shift to track thermally suitable habitats. The same warming rate may yield velocities that vary by more than an order of magnitude in complex terrain because climate velocity is inversely related to topographic steepness and the strength of spatial temperature gradients (28).

Resolution of these issues is needed for designing conservation strategies given the high likelihood of climate warming through at least midcentury and significant societal investments (i.e., billions of US\$) to preserve cold-water species across broad geographic areas (29). Here, we estimate historical stream warming rates and climate velocities throughout the mountainous northwestern United States where concerns about

the region's iconic salmonid fishes and other cold-water species motivated extensive temperature monitoring efforts in recent decades (Fig. 1). Those estimates are combined with large occurrence databases for native and nonnative trouts, a benthic nonsalmonid fish, and an amphibian to describe the thermal environments these cold-water species occupy in mountain headwaters. Counter to widespread beliefs about thermal habitat loss in mountain streams, we find these environments to be highly resistant to temperature increases and many seem poised to serve as climate refugia this century. The implications for conservation planning are widespread and are discussed with key remaining uncertainties for cold-water biodiversity in mountain landscapes.

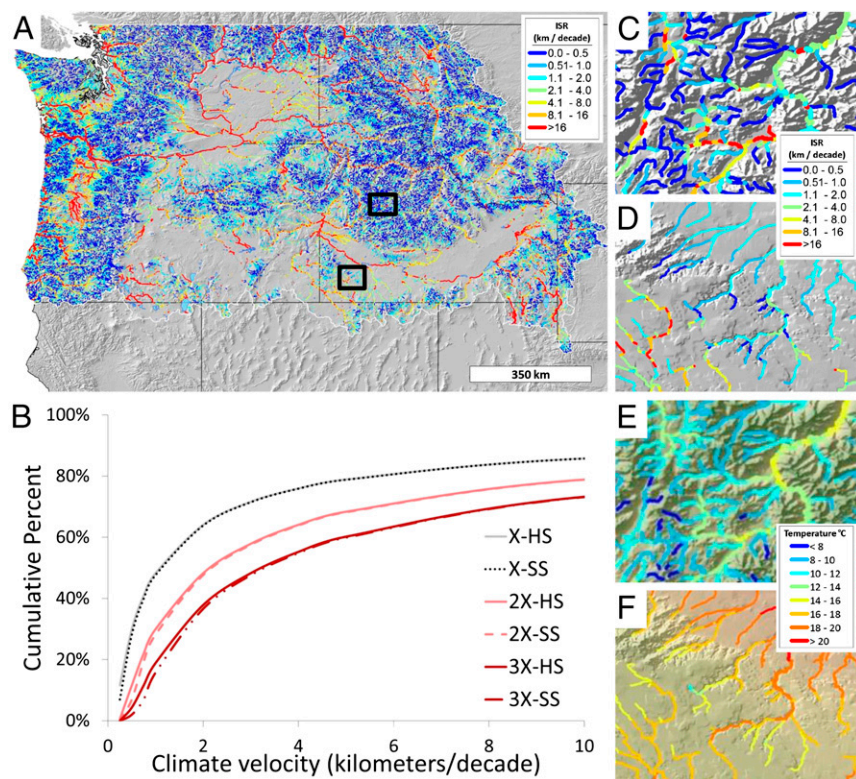


Fig. 2. Stream climate velocity scenario showing isotherm shift rates based on the historical warming rate for 1968–2011 (A; X-HS scenario). Cumulative distribution curves summarizing network velocity profiles for six scenarios based on multiples of the historical warming rate (X, 2X, 3X scenarios) and assignment of stream sensitivities to historical values (HS scenarios) or supersensitive values (SS scenarios). Small images show climate velocities in black boxes (C and D) and August stream temperatures for the same locations (E and F).

Results

The 222,000-km network draining the northwestern United States included 923 sites with ≥ 10 y of monitoring data (average monitoring period = 13 y; range = 10–21 y) that were used to estimate stream temperature sensitivity to air temperature variation with site-specific regression models. Air-stream sensitivities varied considerably among sites except for those with August mean temperatures < 10 °C where the average was 0.32 °C/°C (SE = 0.021; Fig. 1 B and C). Sensitivities at sites > 10 °C showed no trend across a wide range of temperatures but averaged 0.50 °C/°C (SE = 0.0077). Multiplication of sensitivity values by the regional August air temperature trend of 0.21 °C/decade for 1968–2011 yielded long-term stream-warming rates. For streams < 10 °C, the warming trend was estimated at 0.067 °C/decade (SE = 0.0045), whereas warmer streams warmed at 0.105 °C/decade (SE = 0.0016).

Climate velocities based on those long-term stream warming rates indicate that isotherms within the regional network shifted at a median rate of 1.07 km/decade (semiquartile range: 0.45 – 3.76 km/decade) during the historical period (X-HS scenario; Fig. 2), which was more than an order of magnitude lower than velocities reported for terrestrial and marine environments during a similar period and air temperature warming rate (30). Scenarios based on two- to threefold increases relative to the historical warming rate caused network velocities to increase in kind, but increasing the sensitivities of the coldest streams (SS scenarios) to represent possible effects of future decreases in snow (31) or warmer groundwater (32) had negligible effects on network-scale velocity profiles (Fig. 2B). The small effect occurred because the coldest streams affected by the sensitivity increase were in the upper extent of the network, where temperature gradients and stream channels are usually steep (28, 33).

Thermal niche plots indicated that the cold-water vertebrates considered here occurred in low-velocity habitats relative to the range of conditions in the network (Fig. 3). Moreover, three native species of conservation concern—bull trout (*Salvelinus confluentus*), cutthroat trout (represented by the Yellowstone cutthroat trout *Oncorhynchus clarkii bouvierii* and westslope cutthroat trout

Oncorhynchus clarkii lewisii), and Rocky Mountain tailed frogs (*Ascaphus montanus*)—occupied a subset of especially cold, low-velocity environments (median velocities 0.33 – 0.48 km/decade) upstream from other species. Those environments appear to be too cold for invasion by brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), competitors that were broadly introduced and established throughout the region during the 20th century (18). Nonnative brook trout (*Salvelinus fontinalis*) occupy thermal niches that are similar to cutthroat trout and bull trout and may displace them from cold streams where they overlap. Ironically, brook trout has been extirpated from portions of its historical range in eastern North America, in part due to invasions by brown trout and rainbow trout (18). In that region, the presence of cold, low-velocity habitats is also likely to be essential for the long-term persistence of brook trout. Cumulative distribution curves described the skewness of the species occurrence locations, especially of the three native headwater species for which $\sim 90\%$ of occurrences were at locations with velocities < 1 km/decade (Fig. 3B). As a result, distributions of those organisms may have to shift relatively short distances this century (~ 1 – 10 km) to track thermal habitats.

Discussion

Slow climate velocities in mountain streams help resolve the paradox that despite decades of grim predictions about climate-induced extinctions of cold-water fauna, documented examples are rare. To be sure, populations of many species are declining along warm-edge boundaries as temperatures increase (14, 34), but those declines may proceed more slowly than previously thought and provide greater hope for persistence of taxa occupying mountain streams. How much hope ultimately depends on the local biophysical context (e.g., whether a nonnative species is locally abundant or whether natal and adult habitats of migratory taxa are widely separated) and the nexus among how much habitat currently exists, how fast it is changing, and how much is needed by populations to persist. From a solely thermal perspective, however, isotherms are shifting slowly enough that many populations should be able to track them where barriers are not an impediment, and in

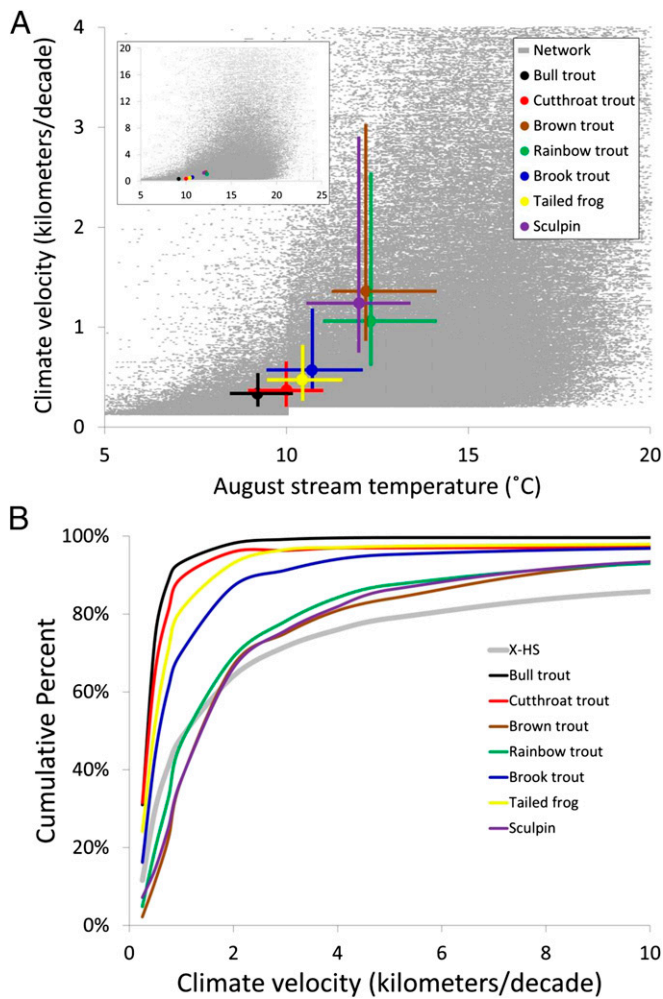


Fig. 3. Scatterplot showing occurrence of cold-water vertebrates relative to network thermal conditions for 1968–2011 (A; X-HS scenario, bars represent semiquartile ranges). Graph shows the cumulative distributions of climate velocities at species locations (B).

some cases, unsuitably cold habitats may exist further upstream to offset losses in warmer areas (19, 35). Moreover, although climate warming will further isolate populations in headwaters, many organisms that inhabit mountain streams are already adapted to an insular existence and could continue to persist for long periods (36).

Coupling spatial-statistical network models with dense temperature datasets makes it routine to accurately predict and map spatial temperature patterns throughout river networks (37, 38), but similar predictive abilities for the wide range of sensitivities among streams (Fig. 1B) remain elusive despite much recent research (9, 39, 40). Except for the low sensitivity of the coldest streams, no trend in mean sensitivity relative to average temperature was apparent (Fig. 1C), and a brief exploratory analysis we conducted yielded only weak correlations ($r < 0.1$) with candidate predictor variables (e.g., elevation, gradient, stream size, baseflow index, and canopy density). The overriding importance of spatial temperature gradients in climate velocity calculations made resolution of the sensitivity issue unnecessary here, but the information would be useful for refining stream climate forecasts. Several mechanisms have been proposed to account for differential stream sensitivity, including groundwater influxes, proximity to persistent snowfields, and forest canopies that create microclimates near streams (9, 10, 32), but these factors are typically studied and modeled at small spatial extents. Larger datasets and analytical tools for expanding

inferential scope while retaining resolution are needed so that those mechanisms could inform forecasts and conservation planning across broader areas. Developing that information using traditional approaches may require significant time and money, so a simpler alternative like geostatistical interpolation of sensitivity values will become increasingly viable as more long-term temperature records become available. It may also be possible to derive sensitivity estimates from models based on subannual changes and short monitoring records (e.g., 1–3 y), which would greatly increase the number of data sites. Doing so, however, will first require comparing estimates derived from subannual and interannual models to ensure that the former are suitable for climate change assessments and are not unduly biased by changing solar angles (9).

Thermal considerations have dominated discussions about climate change effects on cold-water organisms, but of equal or greater importance may be interactions with other climate stressors for which larger uncertainties exist (7). For example, as precipitation patterns and snow accumulation in mountain environments change, so will the magnitude and timing of stream runoff (12, 31). The stream temperature scenario used here was founded on empirical support at more than 16,000 sites, but flow scenarios from hydrologic models are based on sparse monitoring networks of 10s to 100s of sites and predictions require extensive spatial extrapolations that may result in imprecise estimates of network extent and flow dynamics (41). The problem is most acute in headwater streams that are rarely instrumented and have small flow volumes, thereby translating to large relative prediction errors (42). As climate and hydrologic regimes change, so too will stochastic disturbances in high-energy mountain environments where more extreme or frequent droughts, wildfires, floods, and channel disturbances can be expected. Mountain stream communities evolved with dynamic habitats (43), but populations confronted by these changes are likely to require larger habitats to persist than has historically been the case (44). Estimating those habitat sizes and locations that exceed minimum thresholds as temperatures and other factors change simultaneously will be key challenges in the years ahead (19).

Habitat requirements are ultimately a species-specific consideration, which leads to uncertainties about the ecology of mountain streams where cold-water biodiversity is often poorly inventoried and described. Many thousands of kilometers of habitat remain uninventoried even for the most charismatic species like salmonid fishes in a well-studied region such as the northwestern United States (19). Moreover, new cold-water species have recently been described in that region (45), which is indicative of the broader appreciation of cryptic biodiversity that is emerging for mountain streams (46, 47). Extensive spatial surveys and geodatabases of occurrence locations for all species will be needed to complement traditional information about habitat quality and population dynamics for a few species if future conservation efforts are to be comprehensive. Rapid adoption and broad use of inexpensive, sensitive environmental DNA sampling techniques (48, 49) coupled with better phylogeographic treatises (46, 50) will be fundamental to meeting those needs.

It is ironic that the attributes of mountain stream ecosystems often cited as significant climate vulnerabilities—headwater networks hosting insular communities reliant on cold temperatures—may instead be what confers them considerable resistance. Capitalizing on the opportunities thus afforded requires better understanding, databases, and predictive abilities, and much basic work still remains to map and name headwater streams in Earth’s montane regions (42). However, in many data-rich areas of Europe and North America, significant progress can be made simply by organizing disparate datasets into spatially dense databases. Those databases are the foundation for developing the high-resolution stream temperature scenarios and species distribution models that are ultimately required to forecast locations of climate refugia at an extent and resolution relevant to conservation planning. Past experience has taught us the utility of that approach for trout and

Table 1. Summary statistics for 1-km stream reaches within the 222,000-km network of rivers and streams in the northwestern United States

Reach characteristic	Average	Median	SD
Reach slope, %	2.78	1.83	2.72
Mean summer flow, m ³ /s	37.7	0.2	383
August stream temp, °C	14.1	14.2	3.36

stream temperature modeling in the American West (19, 51), and we anticipate similar approaches will prove useful elsewhere. Engaging in efforts to develop those databases also builds stronger relationships and collaborations between researchers and managers as all push toward identifying, prioritizing, and protecting key watersheds and habitats to serve as redoubts from what lies ahead. Mountain streams will provide cold-water taxa an invaluable asset during those times.

Methods

Study Area and Regional Stream Network. The northwestern United States encompasses 794,000 km², a broad elevation range (0–4,200 m), and numerous smaller mountain ranges that constitute the Cascade Mountains and Northern Rocky Mountains. The area is drained by a thermally diverse network of rivers and streams that flow through low-elevation deserts, mid-elevation steppe grasslands, high-elevation forests, and alpine tundra. Within this region, a network that represented habitat for fish and other aquatic vertebrates was delineated from the 1:100,000-scale National Hydrography Dataset-Plus (NHD-Plus) geospatial layer (www.horizon-systems.com/NHDPlus/index.php). Summer flow values were downloaded from the Western US Stream Flow Metrics website (www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml) and linked to each reach in the network. Reaches with summer flows <0.028 m³/s were removed from the network to exclude areas with intermittent flow. We also trimmed reaches from the upper extent of the network once slopes exceeded 10% because geological barriers are common in these areas and often impede upstream migration by vertebrates (52). Application of the slope and flow criteria resulted in a 222,000-km stream network (Table 1 and Fig. 1). High-resolution (1 km) stream temperature scenarios for that network were developed previously through the NorWeST project by applying spatial-statistical stream-network models (51, 53) to monitoring data from 16,388 unique stream temperature sites (www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html). The predictive accuracy of the NorWeST model ($r^2 = 0.91$; root mean square prediction error = 0.98 °C; mean absolute error = 0.62 °C), combined with substantial empirical support, provided a consistent and spatially balanced rendering of temperature patterns and thermal habitat throughout the regional network (Fig. 1A). To describe the thermal habitats associated with recent climatic averages, we used the S1 NorWeST scenario that represented the 19-y (1993–2011) composite of August mean temperatures. An August mean temperature was used because most monitoring data were available for this month, its thermal conditions are strongly correlated with other months, and the summer season is important for growth and survival of mountain stream organisms.

Stream Sensitivity Estimates. The NorWeST website also hosts >150 million hourly stream temperature recordings from >100 natural resource agencies that have passed through a consistent set of quality-assurance procedures. To estimate stream temperature sensitivity to air temperature variation, we queried the NorWeST database to extract data records from sites where the full month of August had been monitored ≥ 10 y. That query yielded 1,039 sites, but 15 were discarded because they occurred immediately downstream of deep reservoirs with cold hypolimnetic releases that decoupled them from ambient climatic conditions. We also discarded 101 sites where lakes encompassed >1% of the upstream watershed to eliminate lake thermal effects. Multiple regression models were developed for each of the remaining 923 sites to predict August mean stream temperature from interannual changes in August air temperature and stream flow following procedures developed previously (9, 22). Air temperature parameters in those regressions constituted the sensitivity estimates. Air temperature data were downloaded from the US Geological Survey (USGS) Regional and Global Climate website (regclim.coas.oregonstate.edu/) and are based on high-resolution (15 km) RegCM3 model historical reconstructions (54). August stream-flow data were obtained for flow gages on unregulated streams nearest the stream-temperature monitoring sites and were downloaded from the USGS National Water Information System (NWIS; waterdata.usgs.gov/usa/nwis/nwis). The multiple regression models accounted for 52% of the variation in stream temperatures at the 923 monitoring sites, and most of this variation (79%) was attributable to air temperature rather than stream flow.

Climate Velocity Scenarios. Reference equations for calculating stream climate velocities were published (28) and require three input values: (i) stream reach slope (%), (ii) lapse rate with elevation (°C/100 m), and (iii) long-term warming rate (°C/decade). To calculate reach-specific velocities, the equation $y = Lx^{-1}$ was used where: y is the climate velocity in km/decade, x is reach slope (%), and L is a coefficient specific to the combination of lapse rate and long-term warming rate (28). Slope values were interpolated from digital elevation models and were associated with each reach in the NHD-Plus data layer. Lapse rates were obtained from NorWeST temperature model fits and averaged 0.47 °C/100 m (SE = 0.026) for streams across the region. Long-term stream-warming rates were derived as the product of the sensitivity parameters described above and the regional air temperature trend of 0.21 °C/decade for the historical period from 1968 to 2011.

Combinations of different warming rates and stream sensitivities formed the basis of six climate velocity scenarios that were considered (Table 2). Scenarios were based on the historical warming rates (designated with an “X”), and faster warming rates were set at double and triple the historical rates (2X and 3X scenarios). Scenarios with sensitivities that matched historical sensitivities were designated “HS,” whereas “SS” was used to designate “super-sensitive” conditions in which insensitive cold streams became as sensitive to air temperature variation as warmer streams.

Biological Datasets. To characterize the thermal environments associated with cold-water species, we referenced site occurrence locations from published biological databases (7, 19) with S1 NorWeST temperature predictions and X-HS velocity estimates from the 1-km stream reaches that encompassed individual sites. We considered seven species: (i) three native species of conservation concern (bull trout = 1,100 sites; cutthroat trout = 927 sites; Rocky Mountain tailed frogs = 953 sites); (ii) three trout species that have been broadly introduced in the region

Table 2. Summary conditions associated with six climate velocity scenarios calculated for streams and rivers in the northwestern United States

Scenario	August temperature, °C	Sensitivity, stream $\Delta^\circ\text{C}/\text{air } \Delta^\circ\text{C}$	Air warming rate, °C/decade	Stream warming rate, °C/decade
X-HS	<10	0.3:1.0	0.2	0.06
	>10	0.5:1.0	0.2	0.10
X-SS	<10	0.5:1.0	0.2	0.10
	>10	0.5:1.0	0.2	0.10
2X-HS	<10	0.3:1.0	0.4	0.12
	>10	0.5:1.0	0.4	0.20
2X-SS	<10	0.5:1.0	0.4	0.20
	>10	0.5:1.0	0.4	0.20
3X-HS	<10	0.3:1.0	0.6	0.18
	>10	0.5:1.0	0.6	0.30
3X-SS	<10	0.5:1.0	0.6	0.30
	>10	0.5:1.0	0.6	0.30

and are regarded as threats to the native taxa [brown trout = 722 sites, a species of conservation concern in the southern portion of its native range in Europe (14); rainbow trout = 1,332 sites, native to the western two-thirds of the study area; and brook trout = 3,061 sites, a species of conservation concern in its native range of eastern North America (18)]; and (iii) the native slimy sculpin (*Cottus cognatus* = 458 sites), a glacial relic species for which the taxonomy is uncertain in western North America (46). Thermal conditions at species locations were summarized in scatterplots and cumulative distribution curves. Distributions

of climate velocities were strongly skewed by a small number of high values, so we used medians and semiquartile ranges (i.e., 25th to 75th quartiles) as descriptors of central tendency and variability.

ACKNOWLEDGMENTS. This research was supported by the US Forest Service Rocky Mountain Research Station and grants from the US Fish and Wildlife Service's Great Northern and North Pacific Landscape Conservation Cooperatives.

- Korner C, Paulsen J, Spehn EM (2011) A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alp Bot* 121(2):73–78.
- Elsen PR, Tingley MW (2015) Global mountain topography and the fate of montane species under climate change. *Nat Clim Chang* 5(8):772–776.
- La Sorte FA, Jetz W (2010) Projected range contractions of montane biodiversity under global warming. *Proc Roy Soc B* 277(1699):3401–3410.
- Dirnböck T, Essl F, Rabitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob Change Biol* 17(2):990–996.
- Dullinger S, et al. (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat Clim Chang* 2(8):619–622.
- Meisner DJ (1990) Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. *Can J Fish Aquat Sci* 47(6):1065–1070.
- Wenger SJ, et al. (2011) Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proc Natl Acad Sci USA* 108(34):14175–14180.
- Comte L, Buisson L, Daufresne M, Grenouillet G (2013) Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshw Biol* 58(4):625–639.
- Luce C, et al. (2014) Sensitivity of summer stream temperatures to climate variability in the Pacific Northwest. *Water Resour Res* 50(4):3428–3443.
- Lisi PJ, Schindler DE, Cline TJ, Scheuerell MD, Walsh PB (2015) Watershed geomorphology and snowmelt control stream thermal sensitivity to air temperature. *Geophys Res Lett* 42(9):3380–3388.
- Loarie SR, et al. (2009) The velocity of climate change. *Nature* 462(7276):1052–1055.
- Luce CH, Abatzoglou JT, Holden ZA (2013) The missing mountain water: Slower westerlies decrease orographic enhancement in the Pacific Northwest USA. *Science* 342(6164):1360–1364.
- Margesin R, Schinner F (1999) *Cold Adapted Organisms: Ecology, Physiology, Enzymology and Molecular Biology* (Springer-Verlag, Berlin).
- Almodóvar A, Nicola GG, Ayllón D, Elvira B (2012) Global warming threatens the persistence of Mediterranean brown trout. *Glob Change Biol* 18(5):1549–1560.
- Parkinson EA, et al. (2015) Identifying temperature thresholds associated with fish community changes in British Columbia, Canada, to support identification of temperature sensitive streams. *River Res Appl* 32(3):330–347.
- Villegier S, Blanchet S, Beauchard O, Oberdorff T, Brosse S (2011) Homogenization patterns of the world's freshwater fish faunas. *Proc Natl Acad Sci USA* 108(44):18003–18008.
- Pont D, Hughes RM, Whittier TR, Schmutz S (2009) A predictive index of biotic integrity model for aquatic-vertebrate assemblages of western U.S. streams. *Trans Am Fish Soc* 138(2):292–305.
- Fausch KD (2008) A paradox of trout invasions in North America. *Biol Inv* 10(5):685–701.
- Isaak DJ, Young MK, Nagel DE, Horan DL, Groce MC (2015) The cold-water climate shield: Delineating refugia for preserving salmonid fishes through the 21st century. *Glob Change Biol* 21(7):2540–2553.
- Culumber ZW, Shepard DB, Coleman SW, Rosenthal GG, Tobler M (2012) Physiological adaptation along environmental gradients and replicated hybrid zone structure in swordtails (Teleostei: Xiphophorus). *J Evol Biol* 25(9):1800–1814.
- McKelvey KS, et al. (2016) Patterns of hybridization among cutthroat trout and rainbow trout in northern Rocky Mountain streams. *Ecol Evol* 6(3):688–706.
- Isaak DJ, Wollrab S, Horan D, Chandler G (2012) Climate change effects on stream and river temperatures across the northwest US from 1980–2009 and implications for salmonid fishes. *Clim Change* 113(2):499–524.
- Orr HG, et al. (2014) Detecting changing river temperatures in England and Wales. *Hydro Processes* 29(5):752–766.
- Mountain Research Initiative EDW Working Group (2015) Elevation-dependent warming in mountain regions of the world. *Nat Clim Chang* 5(5):424–430.
- Wu H, et al. (2012) Projected climate change impacts on the hydrology and temperature of Pacific Northwest rivers. *Water Resour Res* 48(11):W11530.
- Null SE, Viers JH, Deas ML, Tanaka SK, Mount JF (2013) Stream temperature sensitivity to climate warming in California's Sierra Nevada: Impacts to coldwater habitat. *Clim Change* 116(1):149–170.
- Ficklin DL, et al. (2014) Climate change and stream temperature projections in the Columbia River Basin: Biological implications of spatial variation in hydrologic drivers. *Hydro Earth Syst Sci Discuss* 11(6):5793–5829.
- Isaak DJ, Rieman BE (2013) Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. *Glob Change Biol* 19(3):742–751.
- Barnas KA, Katz SL, Hamm DE, Diaz MC, Jordan CE (2015) Is habitat restoration targeting relevant ecological needs for endangered species? Using Pacific salmon as a case study. *Ecosphere* 6(7):110.
- Burrows MT, et al. (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334(6056):652–655.
- Stewart IT (2009) Changes in snowpack and snowmelt runoff for key mountain regions. *Hydro Processes* 23(1):78–94.
- Kurylyk B, Kerry L, MacQuarrie TB, Voss CI (2014) Climate change impacts on the temperature and magnitude of groundwater discharge from shallow, unconfined aquifers. *Water Resour Res* 50(4):3253–3274.
- Leopold LB, Wolman MG, Miller JP (1964) *Fluvial Processes in Geomorphology* (W. H. Freeman, San Francisco).
- Comte L, Grenouillet G (2013) Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography* 36(11):1236–1246.
- Al-Chokhachy R, Alder J, Hostetler S, Gresswell R, Shepard B (2013) Thermal controls of Yellowstone cutthroat trout and invasive fishes under climate change. *Glob Change Biol* 19(10):3069–3081.
- Whiteley AR, et al. (2010) Genetic variation and effective population size in isolated populations of coastal cutthroat trout. *Conserv Genet* 11(5):1929–1943.
- Isaak DJ, et al. (2014) Applications of spatial statistical network models to stream data. *WIREs Water* 1(3):277–294.
- Ver Hoef JM, Peterson EE, Clifford D, Shah R (2014) SSN: An R package for spatial statistical modeling on stream networks. *J Stat Softw* 56(3):1–45.
- Kelleher C, et al. (2012) Investigating controls on the thermal sensitivity of Pennsylvania streams. *Hydro Processes* 26(5):771–785.
- Kanno Y, Vokoun JC, Letcher BH (2014) Paired stream–air temperature measurements reveal fine-scale thermal heterogeneity within headwater brook trout stream networks. *River Res Appl* 30(6):745–755.
- Wenger SJ, Luce CH, Hamlet AF, Isaak DJ, Neville HM (2010) Macroscale hydrologic modeling of ecologically relevant flow metrics. *Water Resour Res* 46(9):W09513.
- Bishop K, et al. (2008) Aqua Incognita: The unknown headwaters. *Hydro Processes* 22(8):1239–1243.
- Dunham JB, Young MK, Gresswell RE, Rieman BE (2003) Effects of fire on fish populations: Landscape perspectives on persistence of native fishes and nonnative fish invasions. *For Ecol Manage* 178(1):183–196.
- Verboom J, et al. (2010) Population dynamics under increasing environmental variability: Implications of climate change for ecological network design criteria. *Landscape Ecol* 25(8):1289–1298.
- Lemoine M, et al. (2014) Cottus schitsuumsh, a new species of sculpin (Scorpaeniformes: Cottidae) in the Columbia River basin, Idaho-Montana, USA. *Zootaxa* 3755(3):241–258.
- Young MK, McKelvey KS, Pilgrim KL, Schwartz MK (2013) DNA barcoding at riverscape scales: Assessing biodiversity among fishes of the genus Cottus (Teleostei) in northern Rocky Mountain streams. *Mol Ecol Resour* 13(4):583–595.
- Balint M, et al. (2011) Cryptic biodiversity loss linked to global climate change. *Nat Clim Chang* 1(6):313–318.
- McKelvey KS, et al. (2016) Sampling large geographic areas for rare species using environmental DNA (eDNA): A study of bull trout occupancy in western Montana. *J Fish Biol* 88(3):1215–1222.
- Thomsen PF, Willerslev E (2012) Environmental DNA – An emerging tool in conservation for monitoring past and present biodiversity. *Biol Conserv* 183(1):4–18.
- Hortal JF, et al. (2015) Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu Rev Ecol Syst* 46(1):523–549.
- Isaak DJ, et al. (2010) Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecol Appl* 20(5):1350–1371.
- Adams SB, Frissell CA, Rieman BE (2000) Movements of nonnative brook trout in relation to stream channel slope. *Trans Am Fish Soc* 129(3):623–638.
- Ver Hoef JM, Peterson EE (2010) A moving average approach for spatial statistical models of stream networks. *J Am Stat Assoc* 105(489):6–18.
- Hostetler SW, Alder JR, Allan AM (2011) *Dynamically Downscaled Climate Simulations over North America: Methods, Evaluation and Supporting Documentation for Users* (US Geological Survey Open-File Report, Reston, VA), Vol 2011-1238.