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Community ecology

The interaction of exposure and warming tolerance determines fish species vulnerability to warming stream temperatures

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Species vulnerability to climate change involves an interaction between the magnitude of change (exposure) and a species's tolerance to change. We evaluated fish species vulnerability to predicted stream temperature increases by examining warming tolerances across the Wyoming fish assemblage. Warming tolerance combines stream temperature with a thermal tolerance metric to estimate how much warming beyond current conditions a species can withstand. Brown trout, rainbow trout and burbot had the lowest warming tolerances and the highest proportion of currently occupied sites that will become unsuitable under predicted temperature increases. These most vulnerable species were coldwater species, but had neither the lowest thermal tolerances nor would they experience the greatest temperature increases. Our results highlight the importance of considering the interaction of exposure and warming tolerance when predicting climate change vulnerability and demonstrate an approach that can be applied broadly.

1. Introduction

One challenge for managing climate change is predicting which species are most vulnerable. Species' vulnerability to warming temperatures is a function of their exposure (i.e. magnitude of warming they will experience), their warming tolerance (i.e. how close current conditions are to their thermal limits) and adaptive capacity (e.g. ability to behaviourally avoid stressful conditions) [1]. Many climate change studies focus on predicting future exposure, but incorporating species physiological warming tolerances improves predictions [2,3].

Ectotherms, such as stream fishes, are highly sensitive to their thermal environment and warmer stream temperatures alter fish species distributions [4,5]. Coldwater species are assumed to be at high risk from warming due to their low thermal tolerance, restricted distribution and the lack of connectivity among the headwater systems they inhabit [6]. However, recent work suggests that the high-elevation streams inhabited by many coldwater fish species are relatively insensitive to warming and may serve as climate refugia [7]. While the exposure of coldwater fishes in montane streams is less than had been expected based solely on air temperatures, even moderate warming could be detrimental if a species has a low warming tolerance because it occurs in habitat at the edge of its thermal tolerance.

A global study of freshwater fishes suggests climate change vulnerability will be primarily determined by exposure, but it is not clear how well these results translate to the local scale, especially where elevational gradients are

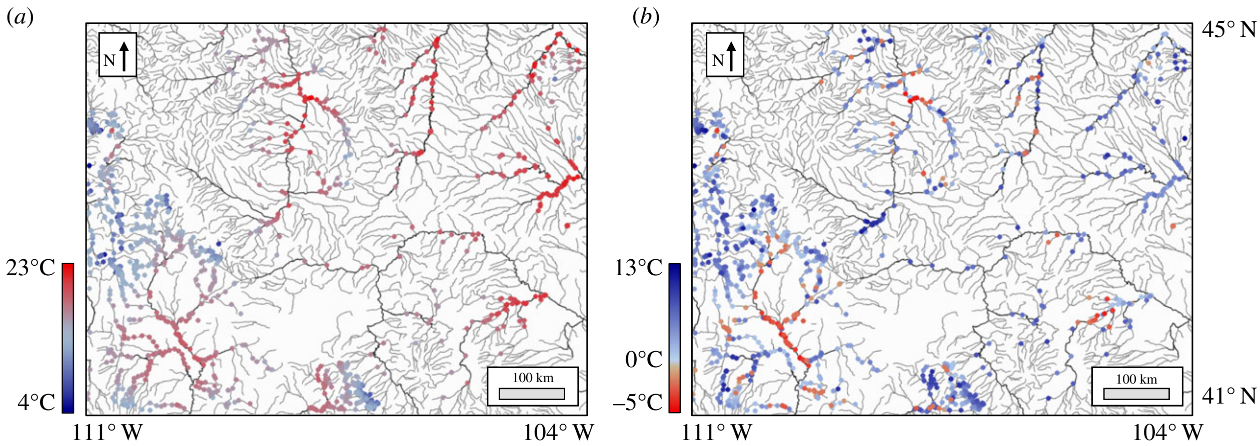

Figure 1. (*a*) Current modelled mean August temperature for all fish sites. (*b*) Lowest warming tolerance among the species present at each site for 2080 scenario.

present [3]. We combined occurrence data, modelled stream temperature data and fish species warming tolerances to evaluate the vulnerability of fishes to stream warming in a high-elevation state, Wyoming.

2. Methods

We gathered fish occurrence data for 1879 sites across Wyoming from the Wyoming Game and Fish Department. Stream temperatures were derived from models generated by the United States Forest Service for the western United States at a 1 km resolution (http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html) [8]. We used modelled historical (1993–2011) mean August temperatures to represent current conditions. This time period (1993–2011) corresponds with the timing of fish sampling (1989–2015). We examined the potential influence of fish sampling year and found no relationship between warming tolerance and year. For our climate change scenarios, we used projections based on global climate model ensembles for the A1B emissions scenario for mean August stream temperatures for the 2040s (2030–2959) and 2080s (2070–2099) and used scenarios that account for the differential sensitivity among streams in the NorWeST unit [8]. We paired each fish occurrence site with modelled historical and future mean August stream temperature for the 1 km stream reach in which it was located.

Fish species thermal tolerance values were from the Wyoming Temperature Database [9] which was based on laboratory studies that evaluated species thermal tolerances. Species acute and chronic criteria were derived following the approach outlined by Todd *et al*. [10], which is closely based on EPA guidance [11]. This approach entailed using known equations to standardize the results of varying laboratory tests of species' thermal optima and maxima to produce a common acute and chronic criterion for all species with sufficient data. We focused on fish persistence and therefore used a common chronic criterion, the maximum weekly average temperatures (MWAT) that a species could tolerate, as our metric of thermal tolerance. To be included in our analysis, species had to be found at a minimum of 10 sites and have sufficient laboratory results in the Wyoming Temperature Database to calculate an MWAT value. This reduced our analysis to 24 species and 1559 sites (table 1 and figure 1*a*).

We calculated current warming tolerance for each fish species at each site as the difference between site temperature and their upper thermal tolerance (MWAT) [3,12]. We assessed vulnerability to future warming by incorporating predicted temperature increases for 2040 and 2080 climate scenarios.

3. Results

Fish species' MWATs ranged from 18.1°C to 33.0°C (table 1). For coldwater species (i.e. trout and burbot), warming tolerances were lower with the warmest occupied sites corresponding closely to their MWAT. However, most species had higher warming tolerances and occurred at sites with mean August water temperatures substantially below their MWAT (figure 2*a*). Current mean August stream temperatures ($\pm$ s.d.) were 16.2 ± 3.2°C with mean increases of 0.9–1.1°C for 2040 and 1.6–2.0°C for 2080 (table 1 and figure 2*b*). Mean warming tolerances were 1.5–12.2°C for current scenarios and decreased for 2040 (0.4–11.3°C) and 2080 (−0.4–10.5°C) scenarios (table 1 and figure 2*c*). In 2080, six species had sites with predicted mean August temperatures above their MWAT (figure 2*c*). These fish with low warming tolerances were primarily in larger streams at lower elevations (figure 1*b*).

4. Discussion

Several coldwater fish species were highly vulnerable to warming stream temperatures as they currently live very close to their thermal tolerance. For brown trout, rainbow trout and burbot, more than 30% of currently occupied sites would be above their MWAT by 2080. Interestingly, the species with the lowest thermal tolerances (cutthroat and brook trout) were not the most vulnerable, because many of their headwater stream sites are cold and have lower predicted temperature increases [13]. This supports the idea that high-elevation streams provide refugia from warming stream temperatures [7]. Warmwater species were relatively insensitive to warming, some living up to 10° below their chronic thermal tolerance; this reflects the fact that Wyoming is a relatively cold state and suggests warming might even be beneficial for some species.

Previous assessments of climate change effects have also predicted a substantial loss of habitat for coldwater fishes in the Rocky Mountain region. Rahel *et al*. [14] estimated that 26% of the stream distance inhabited by trout would be lost if water temperatures increased by 2°C. This is similar to the predicted 33% and 32% losses for brown and rainbow trout respectively for the 2080 scenario (table 1 and figure 2*c*). However, a key result of our analysis is that habitat loss will not be distributed equally among trout species but will be

Table 1. Fish species, their MWAT (°C), number of stream sites occupied, and mean warming tolerances (WT) and predicted temperature increases for current, and 2040 and 2080 climate change scenarios.

species	MWAT (°C)	sites	current WT (°C)	2040 exposure* (°C)	2040 scenario WT (°C)	2080 exposure* (°C)	2080 scenario WT (°C)
cutthroat trout *Oncorhynchus clarkii*	18.1	473	4.9	0.92	3.9	1.60	3.3
brook trout *Salvelinus fontinalis*	18.3	272	5.1	0.94	4.1	1.64	3.4
brown trout *Salmo trutta*	19.3	257	3.1	1.00	2.1	1.76	1.4
rainbow trout *Oncorhynchus mykiss*	19.4	230	3.2	1.03	2.2	1.83	1.4
burbot *Lota lota*	19.6	21	1.5	1.08	0.4	1.92	−0.4
mountain sucker *Catostomus platyrhynchus*	22	458	5.5	1.03	4.5	1.84	3.7
leatherside chub *Lepidomeda copei*	23.8	10	7.7	0.94	6.7	1.63	6.0
common shiner *Luxilus cornutus*	24.2	30	4.2	1.12	3.1	1.99	2.2
bluehead sucker *Catostomus discobolus*	25	58	8.1	1.01	7.1	1.77	6.3
yellow perch *Perca flavescens*	25	11	4.2	1.09	3.1	1.95	2.3
johnny darter *Etheostoma nigrum*	25.4	45	5.8	1.11	4.7	1.98	3.8
shorthead redhorse *Moxostoma macrolepidotum*	26	87	6.0	1.06	5.0	1.90	4.1
Utah chub *Gila atraria*	26	51	8.4	1.05	7.4	1.85	6.5
flannelmouth sucker *Catostomus latipinnis*	26.2	175	8.5	1.04	7.4	1.90	6.6
white sucker *Catostomus commersonii*	27.7	687	9.6	1.04	8.5	1.86	7.7
central stoneroller *Campostoma anomalum*	27.8	29	7.5	1.13	6.4	2.01	5.5
fathead minnow *Pimephales promelas*	28.8	491	10.0	1.04	9.0	1.86	8.2
smallmouth bass *Micropterus dolomieu*	28.9	36	8.6	1.05	7.5	1.88	6.7
common carp *Cyprinus carpio*	29.8	238	10.3	1.05	9.2	1.88	8.4
rock bass *Ambloplites rupestris*	30.2	12	10.7	1.12	9.6	2.00	8.7
gizzard shad *Dorosoma cepedianum*	30.3	59	9.5	0.92	8.6	1.66	7.9
green sunfish *Lepomis cyanellus*	31.1	25	10.7	0.97	9.7	1.74	9.0
channel catfish *Ictalurus punctatus*	32.4	109	11.9	1.07	10.8	1.92	10.0
plains minnow *Hybognathus placitus*	33	37	12.2	0.92	11.3	1.66	10.5

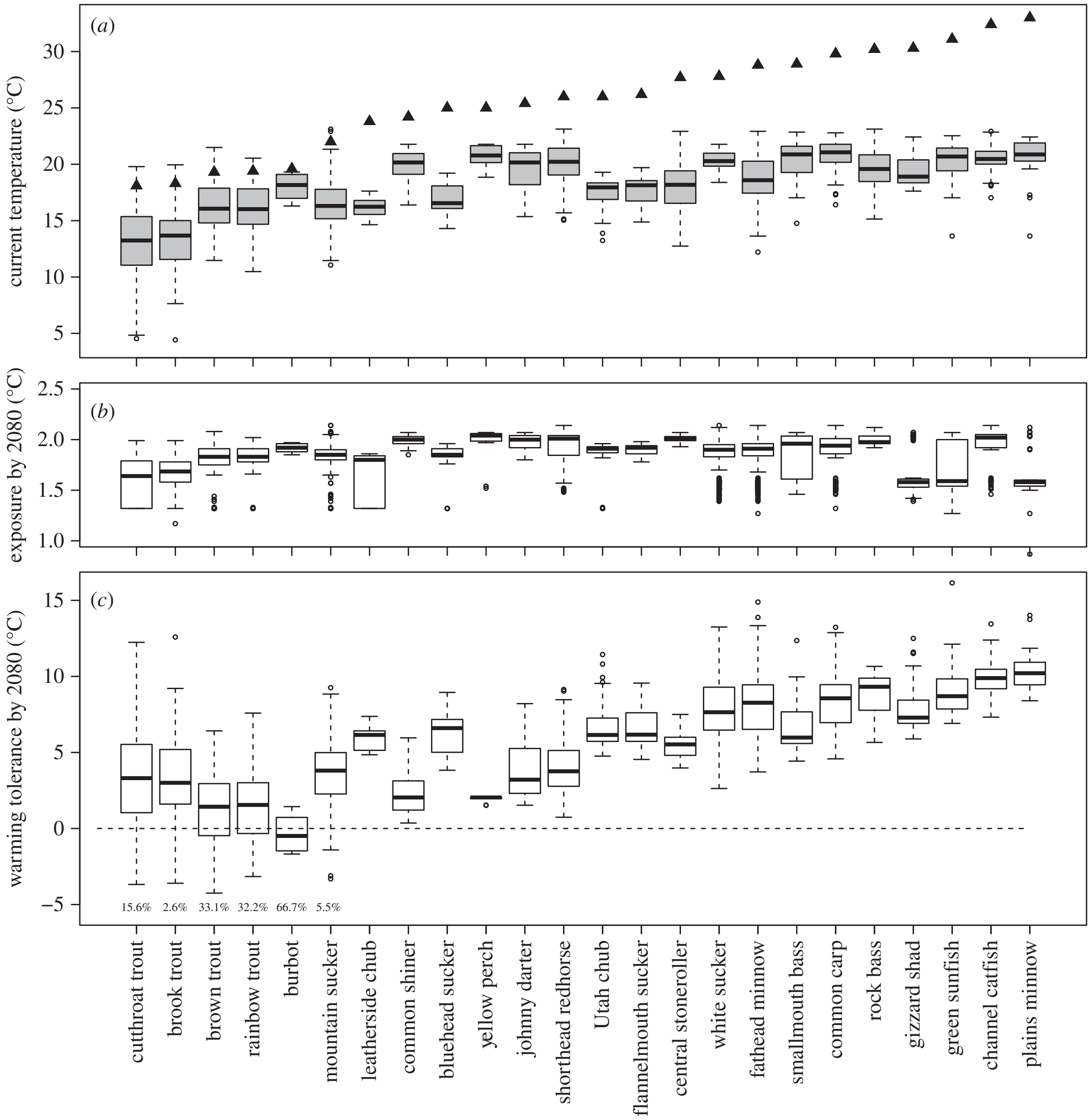

Figure 2. (*a*) Species current temperature distributions with their MWAT marked by a black triangle. (*b*) Temperature increases at occupied sites for the 2080 scenario. (*c*) 2080 warming tolerance values were below zero at some sites for six fish species and the percentage of sites which would be warmer than the species' MWAT is indicated. Species are ordered from lowest to highest MWAT. Circles are boxplot outliers.

higher for brown and rainbow trout compared with brook and cutthroat trout. The higher vulnerability of nonnative brown and rainbow trout to warming stream temperatures could have benefits for native species such as cutthroat trout [15]. However, the loss of 11–15% of cutthroat habitat could also be significant for small, isolated populations that currently exist near their thermal limit at relatively low elevations [5].

The most vulnerable species are common in the transition zone between montane and plains streams. These species may not be able to move upstream to track warmer temperatures due to natural and anthropogenic barriers [16]. For example, burbot are poor swimmers and likely unable to persist in the steep gradients of high-elevation streams. Future work that considers a species's adaptive capacity, for example, traits related to movement ability, would improve vulnerability assessment.

An assumption of our approach is that the occurrence data is representative of a species's current thermal distribution. This might not be the case for species with limited sampling or whose ranges extend beyond Wyoming. For example, Wyoming is on the edge of leatherside chub's distribution and occupied sites are consistently colder than their thermal tolerances. Consequently, leatherside chub has a high warming tolerance that may not be representative of its vulnerability in other parts of its range. Under the current temperature scenario, five species occupy a small proportion of sites (0.4–5.9%) where the current predicted August mean temperature is above their MWAT. This could reflect uncertainty in temperature models, suggest the importance of factors other than temperature (e.g. discharge and species interactions [15]), and demonstrate that species are able to mediate non-optimal temperatures behaviourally [17].

We found that warming tolerance was the most important driver of vulnerability, but exposure also played a role in high-elevation streams highlighting the importance of elevational gradients. A global study of freshwater fishes, focused on latitudinal gradients, found vulnerability was high for north temperate fishes and this was primarily driven by exposure [3]. Our study highlights the additional importance of elevational gradients and the potential for differing results at smaller spatial scales. In addition, our results highlight the importance of considering both exposure and thermal tolerance when determining vulnerability as neither the species experiencing the greatest exposure, nor the most thermally sensitive species were the most vulnerable. This has also been noted in larger-scale studies; tropical insects have high thermal tolerances, but are highly vulnerable to temperature increases as they are already living very close to their thermal limits [2,12]. Combining physiological tolerance data with distribution data is a promising approach that could be applied broadly for a better understanding of species vulnerability to environmental change.

Data accessibility. The dataset supporting this article is available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.76p9017 [18]. R code has been uploaded as electronic supplementary material.

Authors' contributions. A.W.W. and F.J.R. conceived the idea and designed the study; A.W.W. and C.M. collected, analysed and interpreted the data. All authors contributed to writing and revising the manuscript. All authors approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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References

1. Pacifici M *et al.* 2015 Assessing species vulnerability to climate change. *Nat. Climate Change* **5**, 215–225. (doi:10.1038/nclimate2448)
2. Dillon M, Wang G, Huey R. 2010 Global metabolic impacts of recent climate warming. *Nature* **467**, 704–707.
3. Comte L, Olden JD. 2017 Climatic vulnerability of the world's freshwater and marine fishes. *Nat. Climate Change* **7**, 718–722. (doi:10.1038/nclimate3382)
4. Comte L, Grenouillet G. 2013 Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography* **36**, 1236–1246. (doi:10.1111/j.1600-0587.2013.00282.x)
5. Eby LA, Helmy O, Holsinger LM, Young MK. 2014 Evidence of climate-induced range contractions in Bull Trout *Salvelinus confluentus* in a Rocky Mountain watershed, USA. *PLoS ONE* **9**, e98812. (doi:10.1371/journal.pone.0098812)
6. Almodovar A, Nicola GG, Ayllon D, Elvira B. 2012 Global warming threatens the persistence of Mediterranean brown trout. *Glob. Change Biol.* **18**, 1549–1560. (doi:10.1111/j.1365-2486.2011.02608.x)
7. Isaak DJ *et al.* 2016 Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proc. Natl Acad. Sci. USA* **113**, 4374–4379. (doi:10.1073/pnas.1522429113)
8. Isaak DJ *et al.* 2016 *NorWeST modeled summer stream temperature scenarios for the western US*. Fort Collins, CO: Forest Service Research Data Archive. (doi:10.2737/RDS-2016-0033)
9. Peterson CM. 2017 *Development of thermal tiers and regulatory criteria for wyoming stream fishes*, Master's thesis, University of Wyoming, Laramie.
10. Todd AS, Coleman MA, Konowal AM, May MK, Johnson S, Viera NKM, Saunders JF. 2008 Development of new water temperature criteria to protect Colorado's fisheries. *Fisheries* **33**, 433–443.
11. Brungs WS, Jones BR. 1977 Temperature criteria for freshwater fish: protocols and procedures. EPA 600/3-77-061. Duluth, MN: ERS Environmental Research Laboratory, US Environmental Protection Agency, Office of Research and Development.
12. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)
13. Roberts J, Fausch K, Peterson D, Hooten M. 2013 Fragmentation and thermal risks from climate change interact to affect persistence of native trout in the Colorado River basin. *Glob. Change Biol.* **19**, 1383–1398. (doi:10.1111/gcb.12136)
14. Rahel FJ, Keleher CJ, Anderson JL. 1996 Potential habitat loss and population fragmentation for cold water fish in the north platte river drainage of the rocky mountains: Response to climate warming. *Limnol. Oceanogr.* **41**, 1116–1123.
15. 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**, 14 175–14 180. (doi:10.1073/pnas.1103097108)
16. Gibson-Reinemer DK, Rahel FJ, Albeke SE, Fitzpatrick RM. 2017 Natural and anthropogenic barriers to climate tracking in river fishes along a mountain–plains transition zone. *Divers. Distrib.* **23**, 761–770. (doi:10.1111/ddi.12576)
17. Kurylyk BL, MacQuarrie KTB, Linnansaari T, Cunjak RA, Curry RA. 2015 Preserving, augmenting, and creating cold-water thermal refugia in rivers: concepts derived from research on the Miramichi River, New Brunswick (Canada). *Ecohydrology* **8**, 1095–1108. (doi:10.1002/eco.1566)
18. Walters AM, Mandeville CP, Rahel FJ. 2018 Data from: The interaction of exposure and warming tolerance determines fish species vulnerability to warming stream temperatures. Dryad Digital Repository. (doi:10.5061/dryad.76p9017)