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Big biology meets microclimatology: defining thermal niches of ectotherms at landscape scales for conservation planning

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Abstract. Temperature profoundly affects ecology, a fact ever more evident as the ability to measure thermal environments increases and global changes alter these environments. The spatial structure of thermalscapes is especially relevant to the distribution and abundance of ectothermic organisms, but the ability to describe biothermal relationships at extents and grains relevant to conservation planning has been limited by small or sparse data sets. Here, we combine a large occurrence database of >23000 aquatic species surveys with stream microclimate scenarios supported by an equally large temperature database for a 149000-km mountain stream network to describe thermal relationships for 14 fish and amphibian species. Species occurrence probabilities peaked across a wide range of temperatures (7.0–18.8°C) but distinct warm- or cold-edge distribution boundaries were apparent for all species and represented environments where populations may be most sensitive to thermal changes. Warm-edge boundary temperatures for a native species of conservation concern were used with geospatial data sets and a habitat occupancy model to highlight subsets of the network where conservation measures could benefit local populations by maintaining cool temperatures. Linking that strategic approach to local estimates of habitat impairment remains a key challenge but is also an opportunity to build relationships and develop synergies between the research, management, and regulatory communities. As with any data mining or species distribution modeling exercise, care is required in analysis and interpretation of results, but the use of large biological data sets with accurate microclimate scenarios can provide valuable information about the thermal ecology of many ectotherms and a spatially explicit way of guiding conservation investments.

Key words: amphibian; big data; crowd-sourcing; ectotherm; fish; microclimate; species distribution model; stream temperature; thermal niche; topoclimate.

INTRODUCTION

Interest in thermal ecology is growing given concerns about global environmental change, the importance of temperature to many biological processes (Angilletta 2009, Kingsolver 2009, Cooke et al. 2013), and the ease with which temperature data are collected (Angilletta and Krochmal 2003, Selker et al. 2006, Dugdale 2016). Thermal environments are particularly relevant for ectotherms because of their limited ability to physiologically regulate metabolic processes, so these organisms develop behavioral patterns and life histories that adjust to thermal resources over daily, seasonal, and annual cycles (Sunday et al. 2014, Woods et al. 2015). As a result, patterns in ectotherm distribution, abundance, and community structure track spatial temperature gradients at extents that range from the local (Bonneau and Scarnecchia 1996) to the global (Buckley et al. 2012). Intermediate landscape and regional extents, however, may be particularly relevant to species conservation efforts because they encompass fundamental biological units such as locally reproducing populations, metapopulations, and evolutionary lineages (Rieman and Dunham 2000, Manel et al. 2003). Those extents are also likely to encompass the thermal extremes tolerated by many taxa and may reveal warm- and cold-edge distribution boundaries (Opdam and Wascher 2004, Ellender et al. 2016) where the effects of climate warming are most evident and efforts to protect or restore habitat are valuable.

Many temperature-related conservation issues for ectotherms are epitomized by stream-dwelling organisms in mountainous regions. Organisms occur in linear networks where thermal gradients from headwaters to lowland rivers are pronounced and anthropogenic activities in or near streams often exacerbate downstream warming trends by decreasing vegetation shade, abstracting water, or widening channels (Poole and Berman 2001, Nusslé et al. 2015). Societally and ecologically important taxa that frequent mountain landscapes (e.g., cold-water fishes such as trout, salmon, and char) are considered to be temperature sensitive and significant numbers are designated for conservation protection (McCullough et al. 2009, McClure et al. 2013). The overarching importance of thermal regimes to aquatic life has

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led regulatory agencies to set species- and life-stage-specific temperature criteria as water quality standards (Poole et al. 2001, Todd et al. 2008), which may trigger costly regulatory measures if exceeded. Thermal criteria are usually developed from laboratory trials on small numbers of individuals (Selong et al. 2001) but are cost-prohibitive for many species and uncertainties exist about their transferability to wild populations for which fundamental niches are environmentally constrained (Rezende et al. 2014, Verberk et al. 2016). Efforts to develop thermal criteria based on field observations have been attempted but are limited to small numbers of sites with paired temperature and biological measurements (Huff et al. 2005, Beauchene et al. 2014).

As trends of increasing data availability and accuracy in the big data era continue in ecology and climatology (Hampton et al. 2013, 2015), new ways of describing thermal niches and habitat suitability are emerging. Open-access databases host millions of georeferenced species occurrences for thousands of species (e.g., GBIF, Global Biodiversity Information Facility; MARIS, Multistate Aquatic Resource Information System), which could be combined with microclimate surfaces developed from dense networks of miniature temperature sensors deployed across regional landscapes (Ashcroft and Gollan 2012, Holden et al. 2015). The new generation of microclimate models, sometimes referred to as topoclimate models, provide empirically supported interpolations at resolutions of tens to hundreds of meters and rely on data densities that are often an order of magnitude greater than previous climate model scenarios used in bioclimatic assessments (e.g., WorldClim [Hijmans et al. 2005]; PRISM [Daly et al. 2008]). Parallel trends have occurred in stream microclimatology where, for example, the NorWeST project (Isaak et al. 2016*a*) has developed high-resolution temperature scenarios from sensor measurements at >20000 stream and river sites in the American West (data *available online*).[5]

Given the likelihood of increasing global temperatures for the foreseeable future (IPCC 2013), many ectothermic species will be affected and means of developing precise information about locations where environments are thermally constraining are needed for conservation planning. Here, we explore potential synergies between microclimate scenarios and large biological data sets using stream temperature scenarios for a 149000-km network in the U.S. Rocky Mountains and a large compilation of aquatic species surveys (23021 surveys at 13769 sites). Correlative species distribution models (SDMs) are used to link the temperature and biological data sets and parameterize thermal response curves for 14 species of fish and amphibians. Because the approach also facilitates multivariate assessments, we evaluated how inclusion of variables representing other important environmental gradients could affect description of thermal relationships. Information about temperatures associated with the warm-edge boundary of a native species of conservation concern was used with a habitat occupancy model to highlight how conservation investments could be strategically prioritized within the regional network. Results are discussed with regards to conservation planning, future data needs, and caveats associated with correlative models applied to aggregated data sets.

METHODS

Study area

The 399000-km^2 study area covers a portion of the U.S. Rocky Mountains, primarily in Idaho and western Montana (Fig. 1). The region is topographically complex and encompasses environments ranging from mid-elevation steppe grasslands to mountainous forests and alpine zones exceeding 4000-m elevation. Climate is characterized by cold winters with moderate to heavy snow accumulations at high elevations and warm, dry summers. Stream hydrographs are typical of snowmelt-dominated systems, with high flows during spring and early summer and low flows during late summer, fall, and winter. Although urban areas with dense human populations occur at lower elevations in some river valleys, most of the region is sparsely populated. Fish communities are relatively simple and consist of native and introduced members of the families Catostomidae, Cottidae, Cyprinidae, and Salmonidae (Table 1; Meyer et al. 2013, Wallace and Zaroban 2013). The diversity of stream-dwelling amphibians is low with one to two species at many locations (Maxell et al. 2003).

Stream network and habitat covariates

The stream network within the study area was delineated using the 1:100000-scale National Hydrography Dataset Plus (NHD Plus) geospatial layer and originally consisted of 268000 km (data *available online*).[6] Reaches in the network coded as intermittent (i.e., Fcode = 46003) were removed to exclude channels that were unlikely to be used by aquatic vertebrates, which resulted in a 149000-km network for the analysis (Fig. 1). Stream temperature scenarios with 1-km resolution were developed previously in the NorWeST project by applying spatial-stream-network models (Ver Hoef and Peterson 2010) to 20072 summers of temperature monitoring at 7691 stream sites conducted between the years of 1993 and 2011 (Isaak et al. 2016*a*). The predictive accuracy of the NorWeST model (cross validated $r^2 \sim 0.90$; cross-validated RMSPE ~1.0°C; Isaak et al. 2010), combined with substantial empirical support, provided a consistent and spatially balanced rendering of temperature patterns and thermal habitat throughout the study area. Scenarios depicting mean August temperatures were downloaded from the NorWeST website and linked to individual stream reaches in the NHD Plus layer

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[5] www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html

[6] www.horizon-systems.com/NHDPlus/index.php

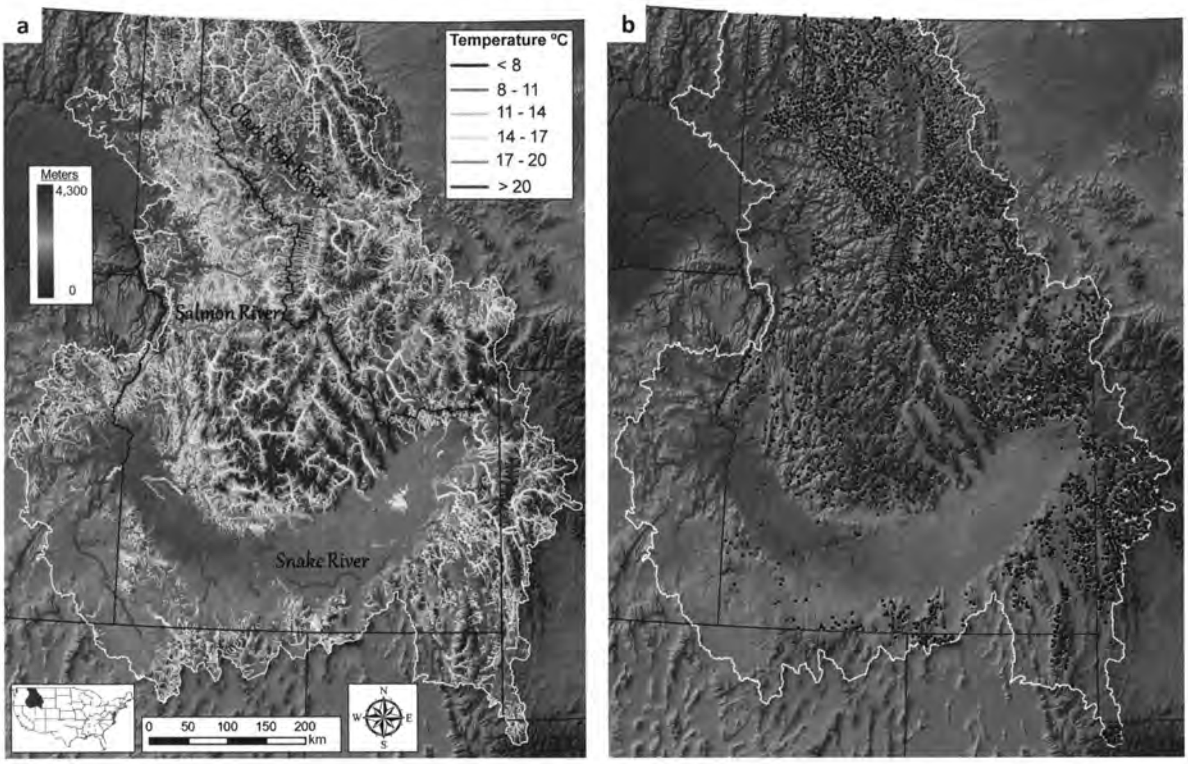

FIG. 1. (a) August stream temperature scenario for the 149000-km study area network. (b) The 13769 unique sites (black dots) where species presence–absence data were collected. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1. Species for which thermal relationships were described in Rocky Mountain streams.

Species	Common name	Order	Occurrences
Rhinichthys cataractae	longnose dace	Cypriniformes	169
Rhinichthys osculus	speckled dace	Cypriniformes	52
Richardsonius balteatus†	redside shiner	Cypriniformes	129
Catostomus catostomus	longnose sucker	Cypriniformes	235
Prosopium williamsoni	mountain whitefish	Salmoniformes	2026
Oncorhynchus clarkii	cutthroat trout	Salmoniformes	11543
Oncorhynchus mykiss†	rainbow trout	Salmoniformes	3977
Oncorhynchus tshawytscha	chinook salmon	Salmoniformes	1728
Salmo trutta‡	brown trout	Salmoniformes	1228
Salvelinus confluentus	bull trout	Salmoniformes	2809
Salvelinus fontinalis‡	brook trout	Salmoniformes	7036
Cottus cognatus	slimy sculpin	Scorpaeniformes	759
Ascaphus montanus	Rocky Mountain tailed frog	Anura	957
Rana luteiventris	Columbia spotted frog	Anura	214

† Nonnative to some streams within the study area.
‡ Nonnative to all streams within study area.

(see footnote 5). Mean August temperature was used because the brief summer season is important for growth and survival of organisms in mountain streams and the species occurrence data sets we used were collected during the summer when streams are accessible. Because biological responses to temperature could be mediated by strong headwater-to-lowlands gradients in channel slope and stream size that affect species distributions (Rahel and Hubert 1991, Wenger et al. 2011*a*), measures of these gradients were also considered. Mean summer flow values from the Variable Infiltration Capacity (VIC) hydrologic model were downloaded from the Western U.S. Flow Metrics website (Wenger et al. 2010; data *available online*)[7] and linked to each NHD Plus stream reach.Reach slope was calculated for stream segments between tributary confluences as the drop in elevation divided by segment length and we used slope values already associated with the NHD Plus layer as Value Added Attributes (McKay et al. 2012).

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[7] http://www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml

Species occurrence data

Biological data were aggregated from four sources: (1) a previously constructed database of salmonid occurrences for the U.S. Rocky Mountains (Wenger et al. 2011*b*); (2) the MFISH database developed by Montana Fish, Wildlife, and Parks (*available online*);[8] (3) the Beneficial Use Reconnaissance Program database provided by the Idaho Department of Environmental Quality (*available online*);[9] and (4) a data set of fish and herpetofauna surveys made from 2008 to 2011 in northern Idaho and western Montana (Young et al. 2013). All biological data were collected during the summer because streams in much of the study area are in mountainous settings and winter snow accumulation and spring floods make sampling difficult during other seasons. We combined data from these sources into a single relational database in which collection records were nested within sites because some sites were sampled repeatedly. If two sites were sampled within 50 m of each other, the data were merged and treated as a single site.

To ensure a level of consistency in the database, we filtered the data by (1) inclusion only of samples made between 1985 and 2011; (2) inclusion only of samples made by backpack electrofishing or snorkeling; (3) exclusion of sites with uncertain locality information; (4) exclusion of sites from the largest rivers (>400 km^2 drainage area or > 32 m^3/s mean summer flow) where sampling techniques were likely to be less effective; (5) exclusion of sites where metadata clearly stated that the occurrence of some species had not been recorded; and (6) exclusion of sites that lay outside a species' historical range, except for sport fishes (brook trout, brown trout, and rainbow trout) that have been widely introduced. Historical ranges were based on published distribution maps (Page and Burr 1991, Behnke 2002) and information from U.S. Geological Survey and U.S. Fish and Wildlife Service websites. The final data set included surveys at 13769 sites representing 23021 different sampling events. Each survey location and species occurrence was referenced to the summer flow and slope values of its NHDPlus stream reach, as well as the mean August temperature in that reach during the sample year (c.f. Al-Chokhachy et al. 2013). Stream conditions at collection sites ranged considerably in mean August temperature (3.0°–21°C), reach slope (0–0.30 m/m), and summer flow (0.01–32.4 m^3/s) although most samples were collected from streams smaller than 1 m^3/s, which constituted the majority of the network (Appendix S1).

Analysis and application

Thermal relationships for 14 taxa (Table 1) that had at least 50 records of occurrence and were drawn from more than one watershed to provide a range of stream conditions were described in two ways: (1) logistic regression models that predicted the probability of occurrence using only stream temperature (hereafter "simple models"), and (2) multiple logistic regression models that also included reach slope and summer flow (hereafter "multivariate models"). The models were fit using both linear and quadratic terms for temperature and linear terms for slope and natural-log-transformed flow values based on our prior experience with similar data sets (e.g., Wenger et al. 2011*a*, *b*). To provide consistent comparisons among species, we retained all predictor variables in the multivariate models regardless of their statistical significance. The logistic regressions were fit as multilevel models with random intercepts for site and a second random intercept for the subwatershed where the sample was collected (12-digit hydrologic unit code). We included the site effect because 15% of sites were sampled multiple times and included the subwatershed effect because sites were non-randomly distributed and spatial autocorrelation among clustered sites could bias parameter estimates (Raudenbush and Bryk 2002). No attempt was made to assess interspecific effects in the models due to the database limitations described above, and because of the complexities associated with differences in community composition across the study area. Correlations among the predictor variables used in the multivariate models were moderate (r = 0.46–0.55; Appendix S1) so multicollinearity was not a concern. Simple and multivariate models were compared using Akaike's information criterion (AIC), for which lower scores are better and a two-point change is often interpreted as a substantive model difference (Burnham and Anderson 2002). Classification accuracy of the models was assessed using the area-under-the-curve (AUC) metric, which is not affected by differences in prevalence among species (Manel et al. 2001, Jiménez-Valverde and Lobo 2006). The scores for AUC range from 0.5 to 1.0, with values of 0.5 indicating prediction accuracy no better than random, values of 1.0 reflecting perfect accuracy, and intermediate scores generally being considered poor (<0.7), good (0.7–0.9), or excellent (>0.9; Hosmer and Lemeshow 2000).

Thermal response curves were plotted as a species' occurrence probability relative to mean August stream temperature across the range of values in the data set. For plots associated with the multivariate models, the temperature relationship was conditioned on the mean values of slope and flow at the occurrence sites. Because the height of the occurrence probability curves was a function of species prevalence in the data set (i.e., rare species have lower occurrence probabilities than common species), curves were standardized for comparison by adjusting peak occurrence probabilities to 0.75 (an arbitrary but consistent threshold). We also defined warm and cold "transition temperatures" as points on the standardized curves with 0.5 probabilities where more extreme temperatures resulted in declining occurrence probabilities and thermal habitat suitability.

To demonstrate a conservation application of the temperature relationships, we focused on bull trout, a native

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[8] http://fwp.mt.gov/fishing/mFish/

[9] http://www.deq.idaho.gov/burp

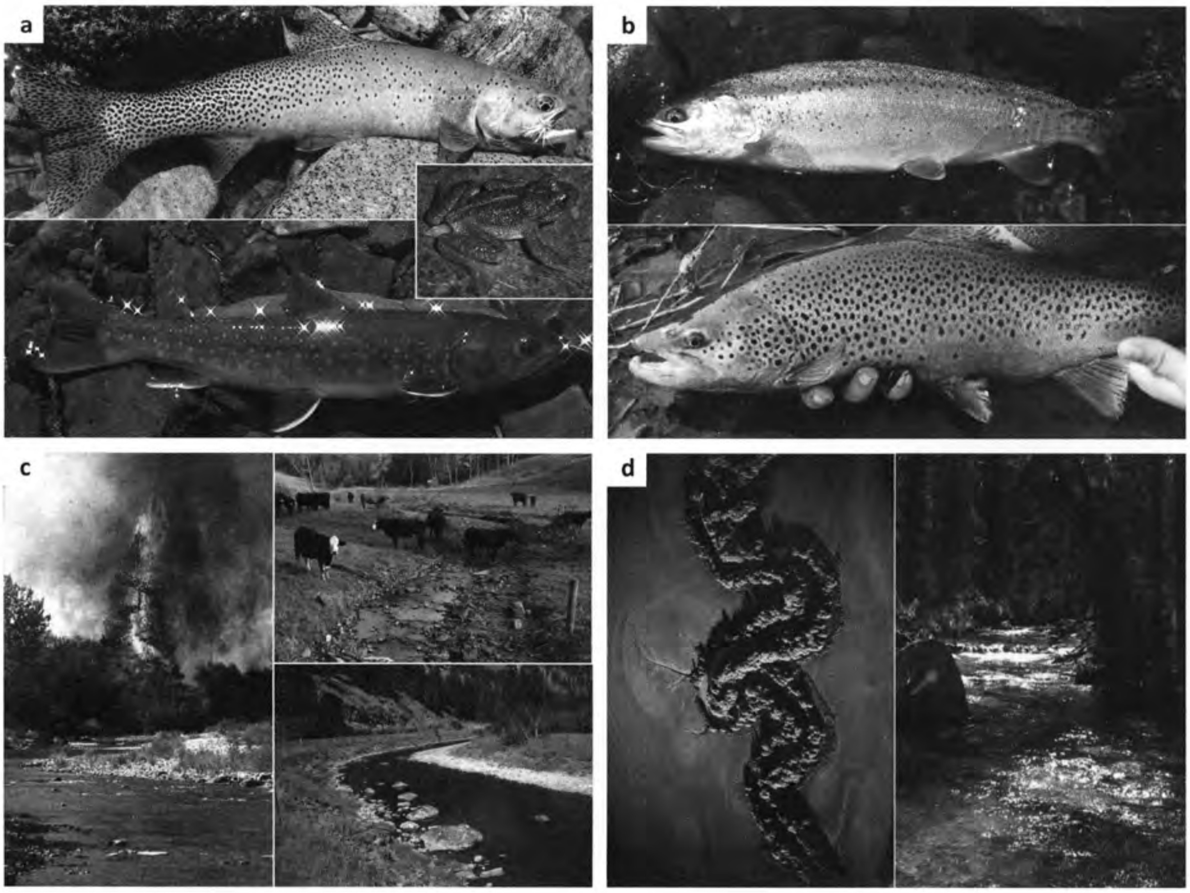

Fig. 2. (a) Species with cold thermal niches like native Rocky Mountain tailed frogs (inset) cutthroat trout (top), and bull trout (bottom) are often replaced by (b) those with warmer niches like rainbow trout (top) and brown trout (bottom) in downstream portions of stream networks. (c) Anthropogenic and natural disturbances may increase stream temperatures but (d) restoration or maintenance of well-shaded stream courses helps ameliorate temperature gains. Photo credits: panel a, Mike Young, Wayne Lynch, Bart Gamett; panel b, Brett Roper; panel c Bill Wolfe, Boise National Forest, Dona Horan; panel d Dan Isaak, Water Encyclopedia. [Colour figure can be viewed at wileyonlinelibrary.com]

species of concern that has been extensively studied and has a well characterized ecology. Bull trout have a cold thermal niche and are often constrained to headwater streams by warm downstream temperatures and other salmonid competitors (Al-Chokhachy et al. 2016, Isaak et al. 2016*a*, *b*, Fig. 2). To highlight temperature-sensitive habitats for bull trout, we summarized a 2°C temperature zone where the species' response curve at the warm-edge boundary indicated low occurrence probabilities and mapped these zones within the regional network. Zone width was a compromise between being overly general and unrealistically precise given the 1.0°C prediction error associated with the underlying stream temperature model. It was unlikely that all potential stream habitats would be occupied by bull trout throughout the study area, so we also combined the temperature zone information with predictions from an accurate occupancy model (Isaak et al. 2015). ArcGIS shapefiles with probabilities of bull trout occupancy were downloaded from the Climate Shield website and probability thresholds of >0.1, >0.5, >0.75, and >0.9 used to provide additional network filters (data *available online*).[10] Finally, we excluded stream reaches in the 2°C zone that were within protected areas like national parks or wilderness areas reasoning that those habitats would either be in pristine condition or unlikely to be candidates for habitat management. Boundaries for protected areas were based on geospatial data obtained from the U.S. Geological Survey Gap Analysis Program (Gergely and McKerrow 2013).

Results

Performance of the simple temperature-only models ranged from poor to excellent (AUC 0.56–0.92; Table 2). Multivariate models usually provided large improvements over the simple models based on AUC values and lower AIC scores (average ΔAIC = 122), a pattern that was most pronounced for species with larger-bodied forms that either permanently or seasonally use larger warmer rivers (e.g., longnose sucker, mountain whitefish, Chinook

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[10] www.fs.fed.us/rm/boise/AWAE/projects/ClimateShield.html

Table 2. Model performance metrics and thermal niche descriptions derived from simple and multivariate models for 14 aquatic species in Rocky Mountain streams.

Species and model	AUC	ΔAIC	Occurrence peak (°C)	Cold transition (°C)†	Warm transition (°C)†
Longnose dace					
Simple	0.86	37	19.0	14.8	–
Multivariate	0.87	0	18.8	13.9	–
Speckled dace					
Simple	0.92	8	17.6	15.0	20.1
Multivariate	0.93	0	17.1	14.7	19.6
Redside shiner					
Simple	0.91	33	–‡	15.1	–
Multivariate	0.93	0	–	14.4	–
Longnose sucker					
Simple	0.81	65	–	13.5	–
Multivariate	0.86	0	–	11.7	–
Mountain whitefish					
Simple	0.76	380	–	15.3	–
Multivariate	0.90	0	–	9.7	–
Cutthroat trout					
Simple	0.56	37	10.6	4.1	17.1
Multivariate	0.56	0	9.1	–	15.9
Rainbow trout					
Simple	0.75	243	20.1	14.0	–
Multivariate	0.83	0	17.0	10.8	–
Chinook salmon					
Simple	0.62	63	–	11.6	–
Multivariate	0.73	0	–	10.9	–
Brown trout					
Simple	0.69	158	18.1	13.6	–
Multivariate	0.73	0	16.2	11.3	–
Bull trout					
Simple	0.60	474	–	–	18.8
Multivariate	0.75	0	–	–	6.2
Brook trout					
Simple	0.57	191	13.7	9.6	17.8
Multivariate	0.63	0	12.8	8.2	17.4
Slimy sculpin					
Simple	0.67	17	15.1	9.6	20.6
Multivariate	0.73	0	14.3	8.5	20.2
Rocky Mountain tailed frog					
Simple	0.65	4	6.4	–	11.8
Multivariate	0.65	0	7.0	–	12.0
Columbia spotted frog					
Simple	0.63	0	13.7	9.5	18.0
Multivariate	0.64	3	13.5	9.2	17.9

Notes: Values not calculated in Cells with dashes. AUC, area-under-the-curve; ΔAIC, Akaike information criterion.

† Transition temperatures not calculated if temperature curve exceeded 0.5 at the maximum or minimum observed temperatures in the study area.

‡ Occurrence peak not calculated if quadratic temperature effect in multivariate model was non-significant (Table 3).

salmon, several trout species). The amount of change in AUC scores for each species was also reflected in differences between the thermal response curves derived from the simple models and the multivariate curves conditioned on slope and flow values (Fig. 3), which highlighted the importance of accounting for factors other than temperature when describing thermal niches. In the multivariate models, significant temperature effects were ubiquitous (all 14 models had a significant linear effect; 9 of 14 models also had a significant quadratic effect) while flow significantly affected 8 species, and slope affected 10 species (Table 3). Steeper stream slopes usually reduced species' occurrence probabilities whereas increasing flows usually increased probabilities, collectively indicating a trend towards greater species richness in larger and less-steep streams. Multivariate models for most species provided good to excellent performance (e.g., AUC > 0.7) but models for four species were relatively poor (Table 2). Those included the two amphibians, which might be expected because neither was fully constrained to stream environments, but also two trout species. In the case of the native cutthroat trout, the species has good dispersal abilities and a wide niche breadth relative to slope, flow, and temperature (Appendix S1) that make it common throughout the study area and challenging to model using presence-absence data. The second trout species, brook trout, has been introduced to many headwater streams but its small body size, limited dispersal abilities, and intolerance of warm temperatures precludes colonization of many suitable habitats, thereby decreasing predictability.

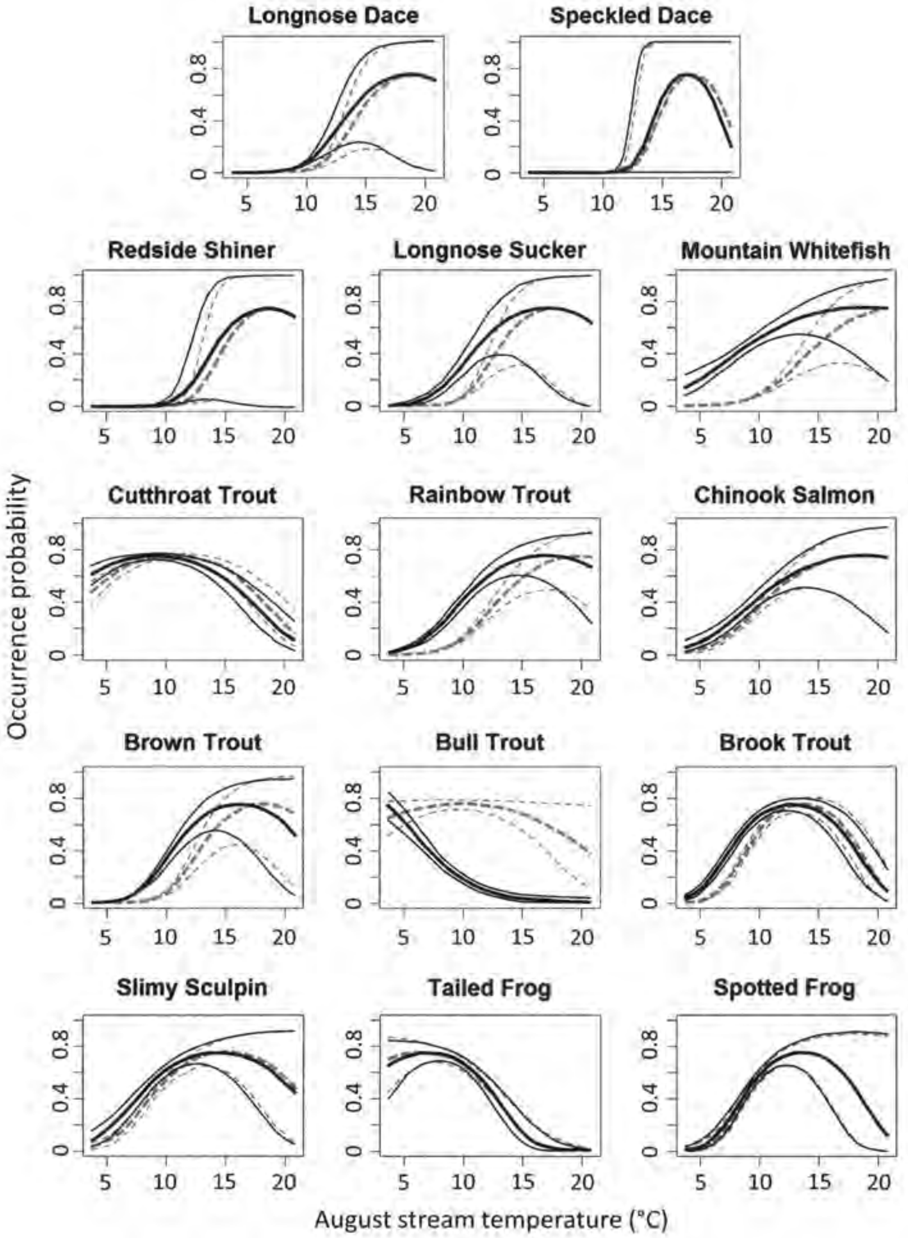


FIG. 3. Thermal response curves for 14 stream species based on simple (dashed lines) and multivariate models (solid lines). Curves associated with the multivariate models were conditioned on the mean values of slope and flow at the species occurrence sites. Thin lines indicate upper and lower 95% confidence intervals.

Thermal response curves indicated that species' occurrence probabilities peaked across a broad range of temperatures and varied considerably in transition temperatures and thermal niche widths (Table 2; Fig. 3). Peak temperatures were not calculated for five species that lacked significant quadratic effects because the highest probabilities for these species occurred in the coldest (bull trout) or warmest (redside shiner, longnose sucker, mountain whitefish, and Chinook salmon) observed temperatures and more extreme thermal conditions than those in the study area were probably required to reveal peaks. Most species showed distinct cold-edge boundaries where confidence intervals were narrow, which was not surprising given the relatively cold temperatures throughout the study area. Interestingly, cold-edge boundaries were apparent even for species like brown trout and rainbow trout that are generally considered cold-water specialists. Thermal curves for the three species with the coldest thermal niches (bull trout, cutthroat trout, and tailed frogs) did not show a cold-edge boundary because their highest occurrence probabilities were in the coldest streams. The skew of those curves

Table 3. Parameter estimates and standard errors (in parentheses) for the multivariate models predicting occurrence of 14 aquatic species in Rocky Mountain streams.

Species	Intercept	Temperature	Temperature^2	Flow†	Slope
Longnose dace	−6.25 (0.30)	0.717* (0.131)	−0.221* (0.104)	0.287* (0.094)	−26.2* (9.12)
Speckled dace	−9.84 (1.17)	2.14* (0.579)	−0.851* (0.325)	−0.332 (0.236)	−55.0* (23.8)
Redside shiner	−8.79 (0.69)	0.946* (0.256)	−0.300 (0.187)	−0.0332 (0.133)	−82.4* (20.8)
Longnose sucker	−6.17 (0.33)	0.438* (0.111)	−0.178 (0.104)	0.160 (0.103)	−57.1* (11.0)
Mountain whitefish	−4.13 (0.18)	0.196* (0.051)	−0.0577 (0.046)	0.810* (0.070)	−23.7* (5.70)
Cutthroat trout	0.67 (0.10)	−0.115* (0.021)	−0.108* (0.018)	0.0876* (0.030)	−3.28* (0.998)
Rainbow trout	−2.15 (0.13)	0.337* (0.035)	−0.136* (0.035)	0.532* (0.048)	−3.42 (2.42)
Chinook salmon	−1.1 (0.21)	0.265* (0.053)	−0.0807 (0.048)	0.0635 (0.076)	−44.5* (6.27)
Brown trout	−4.85 (0.20)	0.461* (0.058)	−0.221* (0.053)	0.438* (0.063)	−15.0* (3.85)
Bull trout	−2.39 (0.13)	−0.383* (0.032)	0.023 (0.035)	0.674* (0.054)	−9.26* (1.85)
Brook trout	−0.74 (0.11)	0.145* (0.023)	−0.247* (0.025)	−0.0242 (0.033)	−14.4* (1.28)
Slimy sculpin	−2.73 (0.13)	0.194* (0.048)	−0.152* (0.058)	0.127* (0.063)	−5.84 (3.14)
Rocky Mountain tailed frog	−3.32 (0.15)	−0.413* (0.046)	−0.208* (0.065)	0.154* (0.060)	3.28 (1.71)
Columbia spotted frog	−4.49 (0.15)	0.256* (0.071)	−0.277* (0.092)	0.0302 (0.088)	−2.28 (3.99)

* $P \leq 0.05$.

† Based on natural-log-transformed values.

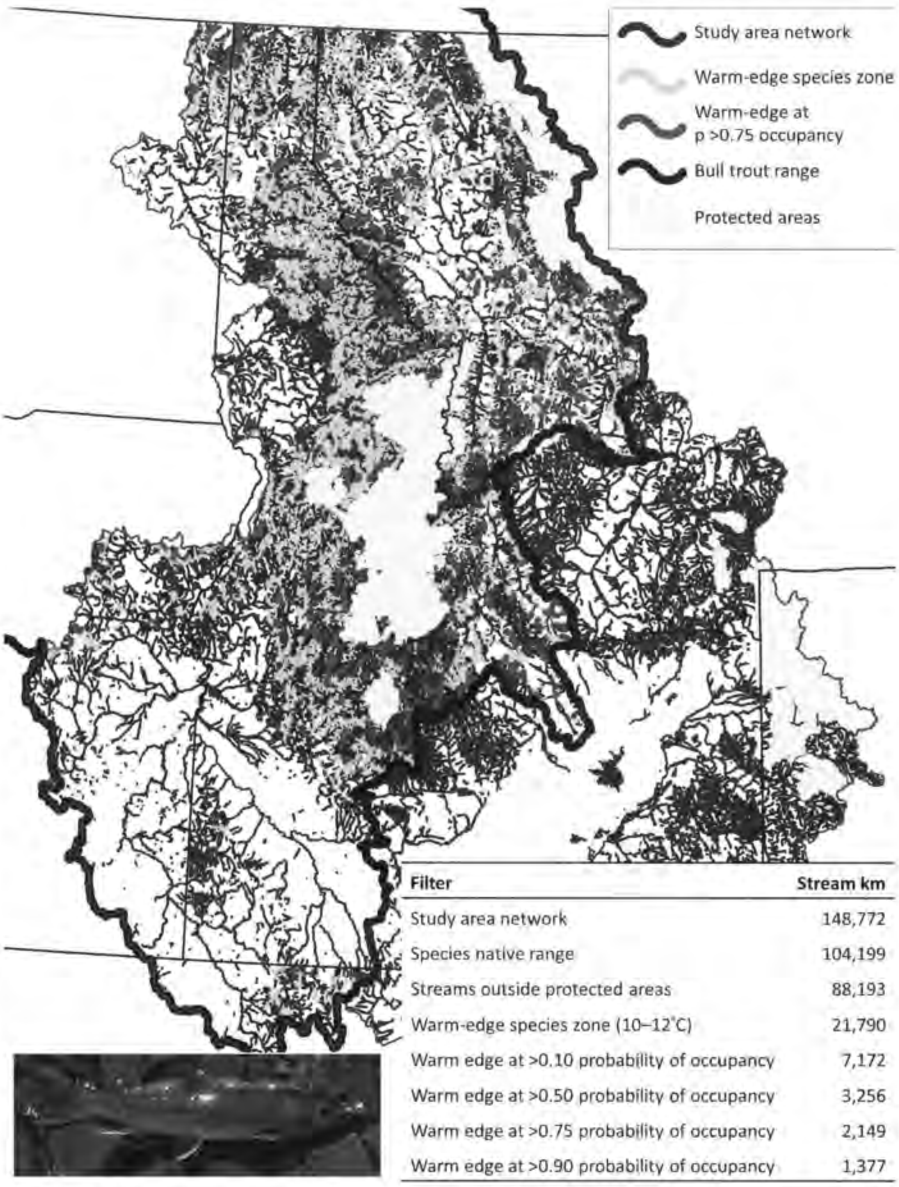
toward cold temperatures, however, created distinct warm-edge boundaries. No other species, except for nonnative brook trout, showed similar warm-edge boundaries (where confidence intervals were usually wide), perhaps because the warmest temperatures in the study area were not acutely stressful for these taxa.

In the conservation application, the multivariate bull trout model was a dramatic improvement over the simple model (ΔAIC = 484) and was used to set a warm-edge boundary temperature zone of 10–12°C because occurrence probabilities in warmer temperatures were low (Fig. 3). Combining that information with network filters pertaining to the species' historical range and protected areas reduced the 149000-km regional network to 21790 km of temperature-sensitive habitats that are not currently in protected areas. Conditioning that result based on bull trout habitat occupancy probabilities further reduced stream lengths to 1377–7172 km, depending on the probability threshold that was applied (Fig. 4).

Discussion

Using a novel combination of microclimate scenarios and large biological data sets, we demonstrate the important role that temperature plays with other environmental gradients in structuring the distributions of ectotherms across a thermally diverse region and network of streams. That insight is not revelatory, as previous studies have demonstrated similar patterns for fishes using stream temperature proxies (e.g., elevation and air temperature; Rahel and Hubert 1991, Wenger et al. 2011*a*, *b*), or for other ectothermic taxa at many scales (Buckley et al. 2012, Woods et al. 2015). Here, however, the use of climate and biological survey data sets of unprecedented density and resolution across a broad extent enabled not only the discernment of biothermal relationships but the mapping of thermally sensitive habitats in ways relevant to conservation planning at landscape and regional scales. Subsequent work is needed to fully refine the approach for individual species or communities of organisms but it is an important step towards providing the spatial specificity and strategic context that could assist in siting costly restoration projects (Buktenica et al. 2013, Williams et al. 2015). Future refinements could involve more complete models that integrate a broader array of environmental characteristics to improve predictive accuracy, development of more detailed databases that enable examination of species interactions, full characterization of thermal niche response surfaces across the ranges of important predictor variables, and provision of model outputs in user-friendly geospatial map formats to facilitate field applications. For some species, models based on density rather than occurrence may also be needed to better resolve thermal effects and their mediation by local environments (Guillera-Arroita et al. 2015, Weber et al. 2016).

In the cold regional landscape we studied, most species showed distinct cold-edge boundaries and transition temperatures. Viewed within the context of climate change, that suggests upstream habitats could provide important refuges from future temperature increases (Isaak et al. 2015, 2016*b*). Enhancing the ability of fishes to disperse upstream may therefore be a key climate adaptation tactic, and one that can often be achieved in many areas by improving habitat connectivity at stream road crossings or water diversions that act as barriers. In extreme instances, human-assisted migrations into thermally suitable but otherwise inaccessible habitats might also be considered (Thomas 2011). A smaller subset of species exhibited warm-edge boundaries, but these included several native species with cold niches that are of conservation concern within the study area. Different tactics could be emphasized at those boundaries, including protection and restoration of riparian vegetation and instream flows to maximize shade and ameliorate stream warming (Fig. 2; Seavy



Filter	Stream km
Study area network	148,772
Species native range	104,199
Streams outside protected areas	88,193
Warm-edge species zone (10–12°C)	21,790
Warm edge at >0.10 probability of occupancy	7,172
Warm edge at >0.50 probability of occupancy	3,256
Warm edge at >0.75 probability of occupancy	2,149
Warm edge at >0.90 probability of occupancy	1,377

FIG. 4. Subsets of the study area network that corresponded to warm-edge boundaries of potential bull trout habitats outside of protected areas such as national parks and wilderness areas. The study area is at the southeastern extent of the bull trout range in North America. Photo credit: Bart Gamett. [Colour figure can be viewed at wileyonlinelibrary.com]

et al. 2009, Nusslé et al. 2015). Intentionally fragmenting habitats might also be used to protect populations in cooler areas from displacement by nonnative species that often invade from warmer downstream areas (Rahel 2013).

In all instances, information to guide strategic planning will be important because conservation is expensive and needs greatly exceed available resources. Our bull trout example demonstrated how a large network could be filtered to smaller sets of candidate sites using geospatial resources but even with the most restrictive filters, substantial amounts of habitat remained that would be unrealistic to restore. Fortunately, not all habitats need restoration but sorting through them at successively finer scales requires precise local information about habitat impairment and environmental conditions. Management and regulatory communities sometimes have that information but it may not be in geospatial or database formats suitable for efficient spatial analysis, so developing databases and ensuring compatibility with strategic models are important future tasks. Remote sensing is a promising tool that is increasingly used to provide high-resolution local information about vegetation characteristics (Bode et al. 2014, Dauwalter et al. 2015, MacFarlane et al. 2016) and habitat morphology (McKean et al. 2008, Harpold et al. 2015) but requires various forms of calibration to represent the environmental nuances most relevant to ectotherms. Moreover, estimating unimpaired site potential relative to current conditions is a significant challenge for remote sensing or any habitat assessment technique, and one that will only become more difficult as that potential changes in association with climate or other global change agents (Catford et al. 2013).

Another key piece of local information pertains to target species occurrence or that of all species if restoration is motivated by broader biodiversity goals. Despite having >20000 biological samples to draw from in our study, most species had fewer than 1000 occurrences, which were sparse when spread across the study area. Even for species with large samples, most sites were clustered and large gaps occurred throughout their ranges. Ideally, species distribution information would be derived from dense samples spread systematically throughout landscapes to better characterize environmental relationships, determine habitat occupancy, and minimize the distances that model predictions are interpolated among samples. Data sets of that quality and extent were unrealistic until recently but are becoming a reality as coordinated, crowd-sourced, biodiversity surveys using environmental DNA (eDNA) sampling become common (Thomsen and Willerslev 2012, McKelvey et al. 2016) and online databases like GBIF and MARIS continue to grow and facilitate data sharing.

The stream microclimate scenarios used here were unique because of their broad spatial extent and data density, the latter exceeding even that of recently published air microclimate models by an order of magnitude (Ashcroft and Gollan 2012, Holden et al. 2015). Similar microclimatic information is needed in many areas to facilitate conservation planning and cost-effective means of development are available. One option is to densify existing temperature monitoring arrays using inexpensive miniature sensors for which numerous instruments and protocols exist (Angilletta and Krochmal 2003, Holden et al. 2013, Isaak et al. 2013). Spatially dense samples minimize imprecisions associated with interpolation routines that must otherwise rely on covariates to predict temperatures at locations without data (Potter et al. 2013). Miniature temperature sensors have been available for decades but their use in broad field campaigns at landscape or regional extents remains rare, so previous monitoring efforts were usually associated with local projects. Where numerous small projects have occurred, however, opportunities exist to aggregate data into larger databases, which may in turn stimulate coordination of future monitoring as awareness of data availability and gaps spreads through human social networks. The ease of collecting temperature data with modern sensors also lends itself to citizen science endeavors that could greatly expand monitoring networks if complemented by centralized means of capturing the resulting data sets and incorporating data into scenario revisions. Another option for microclimate information may be data sets based on land surface reflectance imagery from the MODIS (Moderate Resolution Imaging Spectroradiometer) satellite that are correlated with surface temperatures of terrestrial (Jin and Dickinson 2010) and aquatic environments (McNyset et al. 2015, O'Reilly et al. 2015). The advantage of MODIS data are their global spatial extent at high resolution (1-km) and daily sampling intervals but relationships to local temperatures varies seasonally and geographically (Oyler et al. 2016) and more research is needed to fully understand potential ecological applications. Use of MODIS data requires local temperature measurements for calibration, although these measurements may be sparse compared to those used for interpolating microclimate surfaces.

Describing thermal relationships for ectotherms using correlative models and occurrence databases brings with it the strengths and weaknesses extensively described in the SDM literature (Araújo and Peterson 2012, Franklin 2013) but several merit additional discussion. One key challenge has been a limited ability to accurately describe ecologically relevant, local, habitat conditions across broad areas using geospatial technologies (Pradervand et al. 2014). For most conservation purposes, having that information at the resolution of local populations rather than individuals is sufficient, but even this remains a daunting task (Bennie et al. 2014). Advances in remote sensing and better data from environmental monitoring programs, coupled with increasing availability of geospatial covariates (Wulder et al. 2012, Hill et al. 2016), will reduce but not eliminate this deficiency, so local field knowledge and judgement will remain important for intuiting model structure and assessing realism. Another challenge is that species occurrence databases aggregated from multiple sources may include false absences associated with non-recording bias or inefficient sampling techniques. Incomplete knowledge about the full complement of species at sampling sites makes it difficult to address inter-specific interactions that may be important mediators of thermal responses. Moreover, if false-absence rates are high, parameter estimates may be biased (Tyre et al. 2003) and more complex occupancy models that account for detection efficiency are needed (MacKenzie et al. 2002). Next-generation biodiversity databases developed using eDNA techniques (Thomsen and Willerslev 2012) may reduce the false-absence issue but the rapid proliferation of eDNA surveys will also lead to a crush of new data that require archiving and maintenance even as researchers and management agencies continue to struggle with these issues for historical data sets (Hampton et al. 2013). And because the density of samples will be high in many areas, spatial autocorrelation among samples will be common and require analysis with techniques like the hierarchical models used here or more complex models that explicitly address spatial structure in residual errors (Beale et al. 2010, Isaak et al. 2014).

CONCLUSION

In a century that will be strongly defined by global warming and environmental change, accurate information about thermalscapes and the defining role that temperature plays in the ecology of ectotherms will be critical for conservation planning. As this study demonstrates, large amounts of data needed to develop useful information may already be available in some areas. The data sets used here were contributed by many individuals from numerous resource agencies and simply required effort by a small technical team for development into the databases that supported this research. Working through that process had an important side benefit of increasing communication among all parties, which helped foster and engage a user community that actively uses the database information and collects new data more efficiently, often by sampling in locations where data were previously sparse. Future database and model iterations will improve the accuracy of predictions, the depth of understanding about temperature constraints on ectotherms in Rocky Mountain landscapes, and help local decision makers that sometimes struggle with knowing how and where to resist or adapt to an overarching threat like climate change (Groves et al. 2012). Larger and more precise data sets will also open new research opportunities because many important ecological questions are associated with differences between fundamental and realized niches and species interactions along thermal gradients (Angilletta 2009, Kingsolver 2009). Thermal ecologists may increasingly find themselves in the happy predicament of not being limited by data, but only by their ability to foment testable and insightful hypotheses as society's need for their services increases.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.1501/full

DATA AVAILABILITY

Data associated with this paper have been deposited in a Dryad digital repository https://doi.org/10.5061/dryad.d0s7k