Global Change Biology **WILEY**

Landscape resistance mediates native fish species distribution shifts and vulnerability to climate change in riverscapes

Michael T. LeMoine[1,2] (iD) | **Lisa A. Eby**[1] | **Chris G. Clancy**[3] | **Leslie G. Nyce**[3] | **Michael J. Jakober**[4] | **Dan J. Isaak**[5]

[1]Wildlife Biology Program, University of Montana, Missoula, MT, USA

[2]Skagit River Systems Cooperative, La Conner, WA, USA

[3]Montana Fish, Wildlife and Parks, Hamilton, MT, USA

[4]Bitterroot National Forest, Hamilton, MT, USA

[5]Rocky Mountain Research Station, USDA Forest Service, Boise, ID, USA

Correspondence
Michael T. LeMoine, Skagit River Systems Cooperative, P.O. Box 368, La Conner, WA 98257-0368, USA.
Email: mlemoine@skagitcoop.org

Funding information
USGS Montana Water Center; Univeristy of Montana; USDA McIntire Stennis, Grant/Award Number: MONZ17004

Abstract

A broader understanding of how landscape resistance influences climate change vulnerability for many species is needed, as is an understanding of how barriers to dispersal may impact vulnerability. Freshwater biodiversity is at particular risk, but previous studies have focused on popular cold-water fishes (e.g., salmon, trout, and char) with relatively large body sizes and mobility. Those fishes may be able to track habitat change more adeptly than less mobile species. Smaller, less mobile fishes are rarely represented in studies demonstrating effects of climate change, but depending on their thermal tolerance, they may be particularly vulnerable to environmental change. By revisiting 280 sites over a 20 year interval throughout a warming riverscape, we described changes in occupancy (i.e., site extirpation and colonization probabilities) and assessed the environmental conditions associated with those changes for four fishes spanning a range of body sizes, thermal and habitat preferences. Two larger-bodied trout species exhibited small changes in site occupancy, with bull trout experiencing a 9.2% (95% CI = 8.3%–10.1%) reduction, mostly in warmer stream reaches, and westslope cutthroat trout experiencing a nonsignificant 1% increase. The small-bodied cool water slimy sculpin was originally distributed broadly throughout the network and experienced a 48.0% (95% CI = 42.0%–54.0%) reduction in site occupancy with declines common in warmer stream reaches and areas subject to wildfire disturbances. The small-bodied comparatively warmer water longnose dace primarily occupied larger streams and increased its occurrence in the lower portions of connected tributaries during the study period. Distribution shifts for sculpin and dace were significantly constrained by barriers, which included anthropogenic water diversions, natural step-pools and cascades in steeper upstream reaches. Our results suggest that aquatic communities exhibit a range of responses to climate change, and that improving passage and fluvial connectivity will be important climate adaptation tactics for conserving aquatic biodiversity.

KEYWORDS
barriers, climate change, fish, mobility, stream warming, temperature

1 | INTRODUCTION

Climate change is becoming one of the greatest drivers of global biodiversity loss (e.g., Bálint et al., 2011; Sala et al., 2000; Thomas et al., 2004; Valtonen et al., 2017), with widely documented impacts on species' phenology and physiology influencing ranges (Parmesan, 2006). Commonly observed are shifts in species distributions poleward and toward higher elevations as surface temperatures and precipitation regimes change (Alofs, Jackson, & Lester, 2014; Lenoir, Gégout, Marquet, De Ruffray, & Brisse, 2008; Parmesan & Yohe, 2003). Species that are able to disperse efficiently and have access to suitable habitats may be able to track shifting conditions but climate tracking for many species will be difficult when one or both of these factors is restrictive (Carroll, Parks, Dobrowski, & Roberts, 2018; Parmesan & Yohe, 2003; Schloss, Nuñez, & Lawler, 2012). Bioclimatic envelope models aid in conservation planning by predicting future species distributions at broad spatial extents but often lack the resolution to make precise local projections or omit important ecological processes that may contribute to differential species responses (Angert et al., 2011; Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Millar, Westfall, Delany, King, & Graumlich, 2004; Tingley, Koo, Moritz, Rush, & Beissinger, 2012). Improving the ability to represent climatic conditions at ecologically relevant scales has long been an area of active research (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Potter, Woods, & Pincebourde, 2013) but more recently, the important roles of species traits and landscape resistance have risen to prominence (Foden et al., 2013). Traits that contribute to a species climate vulnerability may include niche breadth, body size, dispersal abilities, diversity of life history types, generation times and initial range size (Comte, Murienne, & Grenouillet, 2014; Foden et al., 2013; Pacifici et al., 2015). Landscape resistance arises from the interaction of species' traits with the physical configuration of potential habitats, the matrix surrounding habitats, and the distributions and behaviors of competitor species that may interfere with target conservation species (MacLean & Beissinger, 2017; McGuire, Lawler, McRae, Nuñez, & Theobald, 2016; Zeller, McGarigal, & Whiteley, 2012). Understanding the nuances inherent to species distribution shifts will be critical for informing management decisions, such as facilitating dispersal or habitat enhancement (Mawdsley, O'Malley, & Ojima, 2009).

Riverine ecosystems host significant portions of Earth's biodiversity (Altermatt, 2013; Dudgeon et al., 2006) and may be especially vulnerable to climate change given communities that are composed of ectothermic organisms, which inhabit linear dendritic networks that are easily fragmented by natural barriers (e.g., waterfalls, reaches with subsurface flows) or anthropogenic barriers (e.g., dams, water diversions, road culverts). This fragmentation may alter species' ability to track climate changes and persist. Although extensive literature describes the potential climate vulnerabilities of species in river networks, it focuses disproportionately on a relatively small number of popular salmon, trout, and

char species that have cold thermal niches, are large-bodied, and often highly mobile (Heino, Virkkala, & Toivonen, 2009; Lynch et al., 2016). Moreover, many of those cold-water species are capable of inhabiting steep mountain headwater streams where climate velocities and the rate of thermal habitat shifts are slow compared to lowland streams and rivers (Isaak et al., 2016). Mid- to low-elevation areas are where aquatic biodiversity is usually greatest due to the downstream accumulation of species in more benign and productive environments (Isaak, Wenger, Peterson, et al., 2017; Rahel & Hubert, 1991) and are where human populations and habitat alterations are usually most prevalent (Haidvogl et al., 2014; Wohl, Lininger, & Baron, 2017). As a result, an important mismatch occurs between current climate risk assessments for riverine species, the degree to which lotic community members may be affected by environmental change, and our understanding of the resilience of these communities.

Empirical case histories describing historical distribution shifts related to climate change are common for many terrestrial and marine taxa and constitute a strong basis for the concerns around global biodiversity loss (Thuiller, Lavore, Araújo, Sykes, & Prentice, 2005; Tittensor et al., 2010). The most robust and convincing assessments involve at least two thorough inventories of the same set of sites separated by a timespan sufficient for environmental change, and establish important baseline datasets for ongoing study (e.g., Grinnell & Storer, 1924; Moritz et al., 2008). With few exceptions such case histories are relatively rare for riverine fishes and often complicated by instream barriers (but see, Comte & Grenouillet, 2013; Eby, Helmy, Holsinger, & Young, 2014; Hari, Livingstone, Siber, Burkhardt-Holm, & Guettinger, 2006). Here we repeated an extensive late 20th century inventory of fish species occupancy throughout a thermally diverse riverscape where warming trends in recent decades were apparent. We compared changes in site occupancy between two periods, 1993–1995 and 2011–2013, for four fish species using dynamic occupancy models (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003; Popescu, De Valpine, Tempel, & Peery, 2012). The four fish species were selected from the native species pool because they were ubiquitous in the basin to ensure adequate sample sites for trend detection. They also have differences in thermal requirements, body sizes, and dispersal abilities. Initial species distributions and changes in site occupancy between the two surveys were linked to a suite of covariates describing local stream habitats, barriers, climatic, and disturbance conditions. We hypothesized that site occupancy of the four species would change most noticeably near the margins of thermal niches (i.e., warmest or coldest sites) and that the changes would be mediated by thermal requirements and local habitat conditions. Additionally, we hypothesized that colonization rates and climate tracking ability of smaller-bodied, weak-swimming fish would be relatively low and limited by instream habitat barriers compared to larger-bodied salmonid species. Finally, we examined scenarios to assess the potential benefits of reducing fragmentation by removing barriers to facilitate dispersal as a conservation strategy.

2 | MATERIALS AND METHODS

2.1 | Study area and dataset

The Bitterroot basin is a 7,394 km^2 snowmelt runoff-dominated watershed with elevations ranging from 945 to 3,048 m and complex mountain topography surrounding a flat, wide main valley located in western Montana, USA (Figure 1). A relatively small human population occupies the basin and is concentrated on privately owned lands in a few towns and ranches at low elevations along the stream and river valleys. Water extraction for pastoral purposes is common on private lands and diversion structures sometimes block fish passage in smaller streams. Higher elevation lands throughout the remainder of the basin are publicly owned and administered by the U.S. Forest Service for a variety of land use, conservation, and management goals. Long-term monitoring records from weather stations in western Montana and throughout the broader region indicate that air temperatures have increased by approximately 1°C during the last 40 years (Littell et al., 2011; Pederson, Graumlich, Fagre, Kipfer, & Muhlfeld, 2010). This warming has affected the regional hydroclimate of rivers and streams, with well documented trends towards reduced snow pack (Mote, Li,

Lettenmaier, Xiao, & Engel, 2018), earlier snowmelt runoff (Hamlet, Mote, Clark, & Lettenmaier, 2007; Stewart, 2009), lower summer flows (Leppi, DeLuca, Harrar, & Running, 2012; Luce & Holden, 2009), and water temperature warming rates of 0.2–0.3°C per decade during the summer and fall seasons (Isaak et al., 2018). Wildfire activity within the Bitterroot basin and regionally has also increased substantially (Figure 1; Morgan, Hardy, Swetnam, Rollins, & Long, 2001), which enhances water temperature increases in some stream reaches by 1.4–2.0°C above background trends (Holsinger, Keane, Isaak, Eby, & Young, 2014; Mahlum, Eby, Young, Clancy, & Jakober, 2011) and can create episodic inputs of sediment and coarse woody debris (e.g., Burton, 2005; Rhoades, Entwistle, & Butler, 2011).

The ichthyofauna in the Bitterroot basin consists of bull trout (*Salvelinus confluentus*), westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), nonnative eastern brook trout (*S. fontinalis*), nonnative rainbow trout (*O. mykiss*), nonnative brown trout (*Salmo trutta*), mountain whitefish (*Prosopium williamsoni*), large scale sucker (*Catostomus macrocheilus*), longnose sucker (*C. catostomus*), slimy sculpin (*Cottus cognatus*) and longnose dace (*Rhinichthys cataractae*). For our analyses, we selected four native species (bull trout, cutthroat trout, longnose dace, and slimy sculpin) that had
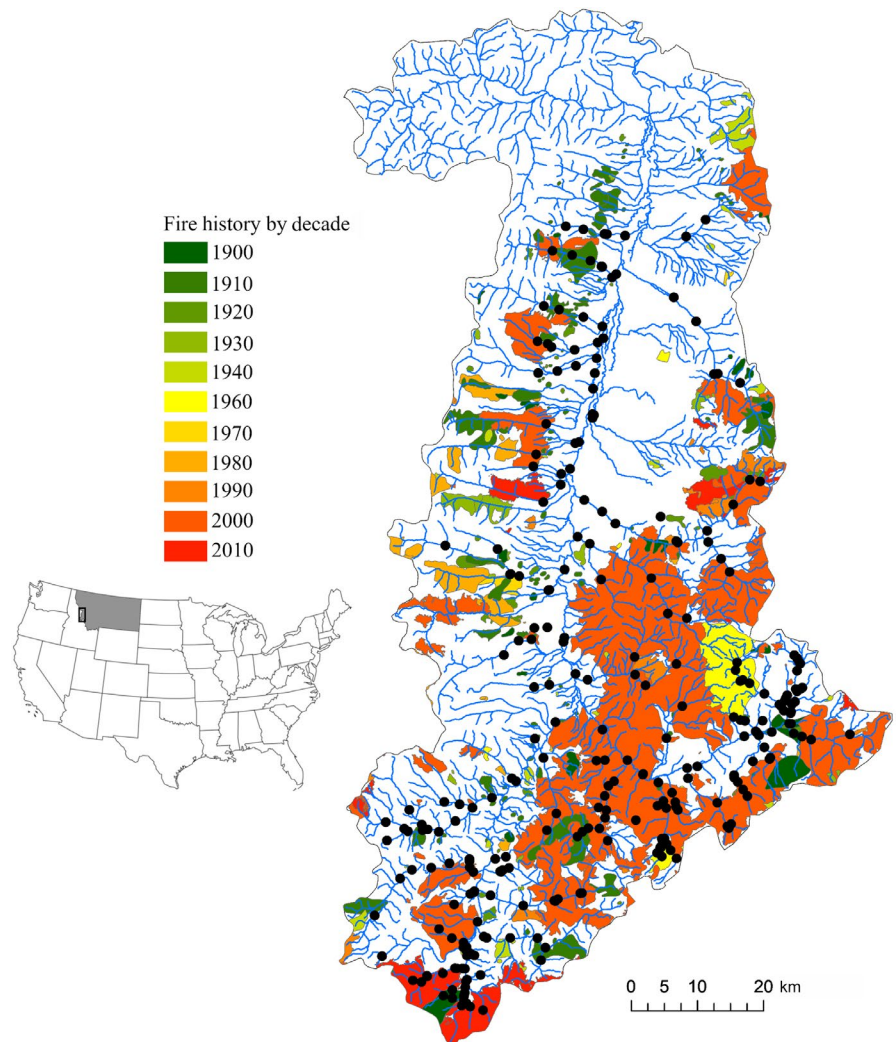
FIGURE 1 Sampling locations (*n* = 280) that were initially visited in 1993–1995 and resampled in 2011–2013 in the Bitterroot River watershed of western Montana, U.S.A. Colored polygons represent wildfire perimeters during the past century. Severe fires occurred in 2000 and 2004 that resulted in major portions of the basin being burned

historically reliable data and were broadly detected across the basin during the early survey period (Figure 2). These species also had different thermal preferences and body sizes. Body size often associates with vagility and should also relate to climate tracking ability (Albanese, Angermeier, & Peterson, 2009). The three other native fish (mountain whitefish, longnose sucker, and largescale sucker) were not regularly netted and reported by the sampling crews over these time periods resulting in less consistent and reliable historical data. We detected them at less than 15% of the sites. Bull trout has the coldest thermal niche of the four species and occurs in abundance only in the coldest headwater streams where summer temperatures are <12°C (Isaak, Wenger, & Young, 2017; Selong, McMahon, Zale, & Barrows, 2001). Adult bull trout often

attain large sizes (e.g., >300 mm) and will seasonally use warm river environments (Howell, Dunham, & Sankovich, 2010), but always migrate to cold headwaters for spawning where juveniles reside and grow for several years (e.g., Fraley & Shepard, 1989; Isaak, Wenger, & Young, 2017; Rieman & McIntyre, 1995). Westslope cutthroat trout also has a cool thermal niche, though one that is not quite as restrictive as bull trout (Bear, McMahon, & Zale, 2007; Isaak, Young, Nagel, Horan, & Groce, 2015), and adults attain large body sizes (>250 mm) and may exhibit either seasonal spawning migrations or headwater resident life history strategies (Shepard, Sanborn, Ulmer, & Lee, 1997). Slimy sculpin is a small-bodied (<140 mm) benthic fish that has a cool thermal niche and occupies summer temperatures of 13–16°C
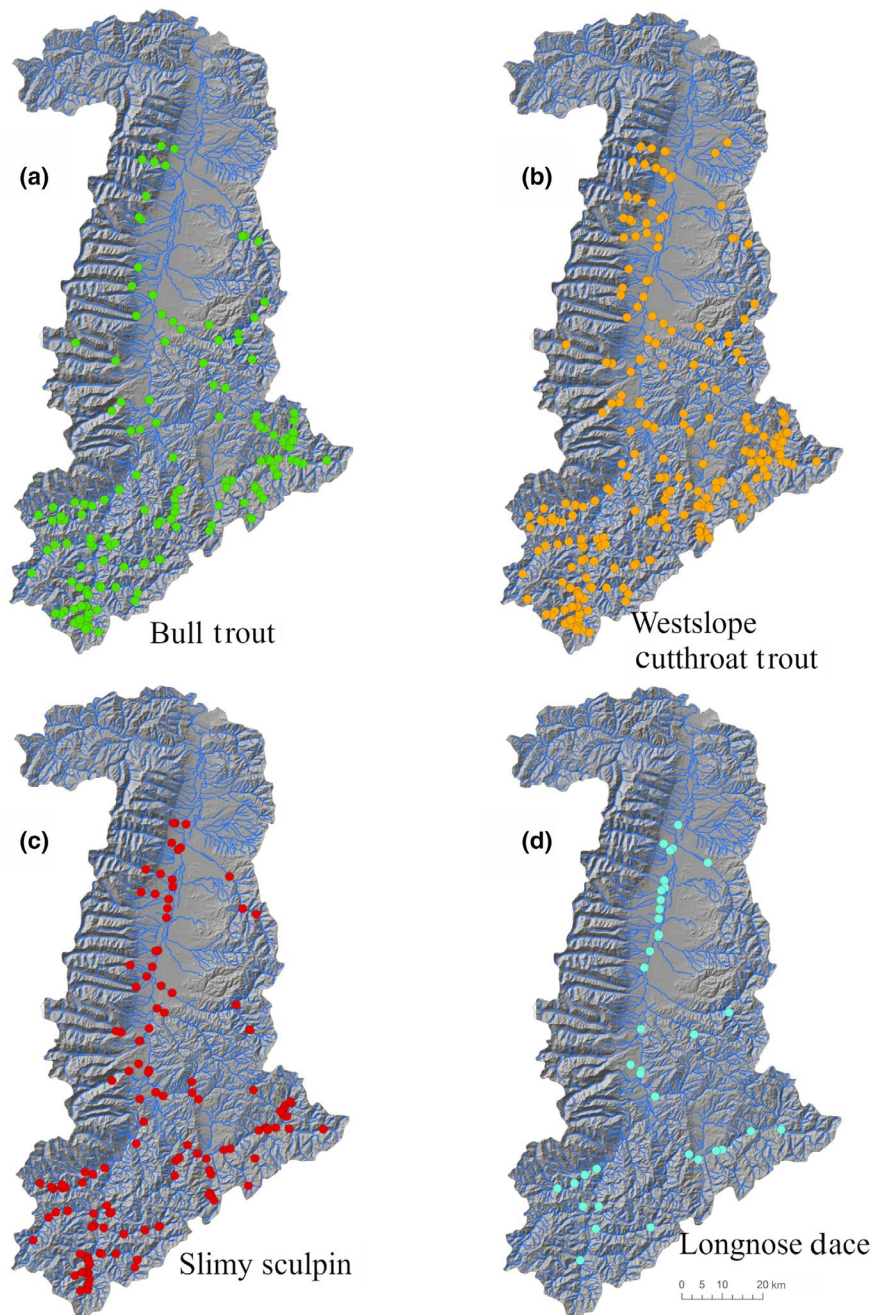
FIGURE 2 Raw detections of (a) bull trout, (b) westslope cutthroat trout, (c) slimy sculpin, and (d) longnose dace in the 1993–1995 dataset

(Adams, Schmetterling, & Neely, 2015; Isaak, Wenger, & Young, 2017). Longnose dace is also small-bodied (<200 mm) and has a comparatively warmer thermal niche, becoming common only where summer temperatures consistently exceed 15°C (Isaak, Wenger, & Young, 2017; Lyons et al., 2009). There is little information on movements of the small-bodied species, but neither of the smaller-bodied species is known to make extensive seasonal migrations (but for sculpin see Schmetterling & Adams, 2004).

Fish community surveys at 280 sites across 81 streams from 1993 to 1995 (Supplemental Materials S1 for full dataset) originally conducted by Montana Fish, Wildlife and Parks (MFWP) and United States Forest Service (USFS) fish biologists were repeated from 2011 to 2013 using the same sampling techniques. Sites were spread throughout the stream network and were located with the help of the same biologists to within 100–200 m across sampling periods (Figure 1). Sampling was done during the late summer when stream flows were lowest and capture efficiencies highest by stunning and netting fish using a backpack-mounted electrofishing unit within small, first through third order streams, and a boat-mounted electrofishing unit in fourth and fifth order streams. Sites were defined as being approximately 10 channel geomorphic units in length (Hawkins et al., 1993) and sites were surveyed one to six times within each of the time periods (e.g., 1993–1995 and 2011–2013). Seventy-seven percent of the sites had at least two visits within each of the time periods and 33% of the sites had three or more visits within each time period providing a robust dataset for estimating probability of detection. Captured fish were identified to species, measured, and enumerated before being released back into streams near their capture sites. Collection and handling procedures were performed in accordance with guidelines specified under scientific collection permits issued to MFWP, USFS, and Michael LeMoine and Lisa Eby by MFWP and protocols approved by the University of Montana Institutional Animal Care and Use Committee (AUP 022-11). Also recorded during the surveys were the amount of sampling effort, stream width, crew members, and gear type for consideration as factors affecting species detectability in the dynamic occupancy modeling framework discussed below (MacKenzie et al., 2003).

2.2 | Habitat covariates

We identified covariates associated with climate, watershed characteristics, and indicators of disturbance that have been shown to potentially affect distributions of stream fishes (Table 1). As with other freshwater fish distribution studies (e.g., Buisson, Thuiller, Lek, Lim, & Grenouillet, 2008; Comte, Buisson, Daufresne, & Grenouillet, 2013; Hari et al., 2006; Rieman et al., 2007; Wenger et al., 2011) our climate variables were associated with indicators of summertime water temperatures (August mean temperature) and stream flows (May snowpack). Our watershed characteristics included reach gradient at site (averaged over 1 km), drainage area, and riparian canopy cover. Stream gradient influences water velocities impacting a fish's ability

to maintain position and energetic costs, and influences other habitat characteristics including substrate size and pool to riffle ratios. Drainage area is a surrogate for stream size that influences site habitat characteristics, such as habitat volume, stream width and depth, and substrate size which also predicts occupancy of these species (Comte & Grenouillet, 2013; Wenger et al., 2011). Greater riparian canopy cover is associated with riparian vegetation, cover and shade (Isaak et al., 2010; Wenger et al., 2011).

Finally, we assessed three disturbance covariates (% watershed burned, road density, and downstream barriers) based relationships described in previous research. Riparian burns are a well-known disturbance on the landscape that can increase stream temperature (Mahlum et al., 2011) and influence fish distributions directly or indirectly through increased stream temperatures through loss of canopy cover that may limit fish presence (Isaak et al., 2010; Rieman et al., 2007). We used road density (km of road miles/km^2 of watershed area) above each site to represent potential sediment inputs (Arnold & Gibbons, 1996).

We defined characteristics of potential natural (cascades and waterfalls) and anthropogenic (culverts, diversion dams) barriers using published literature and governmental reports for each species (westslope cutthroat trout and bull trout: Behlke, Kane, McLean, & Travis, 1991; Bell, Delacy, Paulik, Bruya, & Scott, 1981; Reiser & Peacock, 1995; WDFW, 2009; sculpin: Adams et al., 2015; LeMoine & Bodensteiner, 2014; Utzinger, Roth, & Peter, 1998; see Figure S1). Description of barriers to longnose dace passage are nonexistent, but a body size similar to sculpin suggests they have similar passage requirements (Nislow, Hudy, Letcher, & Smith, 2011). Potential barriers to fish movements were assessed across the Bitterroot basin through reach scale measurements of stream slope using digital elevation models, as well as traversing streams at summer base flow and collecting key characteristics such as, stream bed slope, jump height required to surmount the potential barrier and valley confinement. As downstream stream reaches warm, we expected fish to move upstream into higher elevation, cooler waters. Barriers that reside downstream of a sampling site could impede fish from moving upstream to higher elevations with cooler stream temperatures, thus hindering climate tracking.

2.3 | Occupancy model

Because large adult bull trout and westslope cutthroat trout are seasonally migratory, their occurrence within a reach is not necessarily indicative of residence and therefore site occupancy. For the purposes of our study, we defined site occupancy based on the presence of juvenile and subadult trout <250 mm in length to ensure trout were established in the sampling reach. For bull trout this resulted in eight site occurrences where the capture of bull trout was discounted because only a single large trout >250 mm was captured and smaller bull trout were absent. No similar instances occurred for westslope cutthroat trout because smaller individuals were always present when a large trout was captured

TABLE 1 Descriptive summary statistics of habitat covariates for occupancy, extirpation and colonization for the 280 stream sites in the analyses and the reference for the dataset. Period 1 runs from 1993 to 1995 and period 2 runs from 2011 to 2013

	Mean	Median	Min	Max	Data source
Climate variables					
Period 1: Avg Aug mean temp (°C)	10.7	10.2	6.3	17.3	NoRWeST Stream Temperature Model (http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html, accessed Feb 2014)
Period 2: Avg Aug mean temp (°C)	11.7	11.0	7.1	18.1	
Period 1: Avg May snowpack (cm)	26.3	26.9	0	50.4	SNOTEL Data (http://www.wcc.nrcs.usda.gov/snow/html, accessed Feb 2014)
Period 2: Avg May snowpack (cm)	36.1	34.3	6.8	71.8	
Watershed characteristics					
Reach gradient (% Slope) over 1 km	0.06	0.04	0.00	0.40	NHD Plus dataset derived for stream segments from 30 m DEMs (http://www.horizon-systems.com/nhdplus/NHDPlusV2_home.php, accessed February 2012)
Drainage area above site (km^2)	110.6	32.0	1.2	5,129.8	NHD Plus dataset derived for stream segments from 30-m DEMs (http://www.horizon-systems.com/nhdplus/NHDPlusV2_home.php, accessed February 2012)
Period 1: % Canopy cover	64.2	71.4	0.4	98.4	National Landcover Dataset (NLCD) 1992 and NLCD 2011 (http://www.mrlc.gov/nlcd2001.php.html, accessed February 2012)
Period 2: % Canopy cover	61.4	68.5	0.4	95.7	
Disturbance					
Period 1: Road density (km road/km^2 watershed area)	0.9	0.5	0.0	18.1	http://data.fs.usda.gov/geodata/
Period 2: Road density (km road/km^2 watershed area)	0.9	0.5	0.0	18.1	
% sites with moderate or high severity fire between 1993 and 2013	16.4%				Bitterroot National Forest (BNF) 2001 and Unpublished BNF GIS datasets
No of sites with downstream barriers	Trout 26	Sculpin 135	Longnose dace 161		Field assessments in 2011–2013

at a site. When slimy sculpin and longnose dace were detected at a site, we generally captured at least five individuals at the site suggesting benthic fish were established at the site and not transiting between sites.

Before fitting the occupancy models, we generated a correlation matrix in R version 3.1.2 (Core Team, 2014) to identify and exclude highly correlated covariates ($r > .6$) that could have caused problems with multicollinearity (Dormann et al., 2013). We also standardized covariates to facilitate parameter estimation and interpretation (Harrell, Lee, Califf, Pryor, & Rosati,1984).

We modeled initial site occupancy, site extirpation, and site colonization using dynamic occupancy methods that account for imperfect detection probability developed by MacKenzie et al. (2003). A maximum likelihood modeling procedure relies on detection history data to estimate detection probability (p), initial occupancy (ψ), extirpation (ε), and colonization (γ; MacKenzie et al., 2003). Where p is a matrix of detection probabilities, ψ is a vector of site occupancy probabilities for the first primary sampling period, and ε and γ are matrices of the conditional extirpation

and colonization probabilities. Changes in occupancy may occur between periods when occupied sites become unoccupied (site extirpation) or when unoccupied sites are occupied (site colonization). The dynamic site occupancy is a Markovian process; site extirpation and colonization at time $t + 1$ is dependent upon initial occupancy at time t.

We followed the model structure described by Popescu et al. (2012); the occurrence state of the study species at each site (i) in time period (j), $z(i,j)$, is thus binary and can be modeled as a Bernoulli random variable for the first period such that

$$z_i \sim \text{Bernoulli}(\psi_i),$$

where ψ_i is the probability of a site being initially occupied. The change in occupancy is described by

$$z(i,t)|z(i,t-1) \sim \text{Bernoulli},$$

$$\{z(i,t-1)(1-\varepsilon_{i,t-1})+[1-z(i,t-1)]\gamma_{i,t-1}\},$$

where $\varepsilon_{i,t-1}$ and $\gamma_{i,t-1}$ are the site- and time-specific probabilities of local extinction and colonization, respectively. The observation process is conditional upon the state of the site and is modeled as

$$y(i,t)|z(i,t) \sim \text{Bernoulli}[z(i,t)pt].$$

Thus, the observed "presence/absence" data (y_{ij}) confound the true distribution (represented by z_i) and the detection process (represented by detection probability, p; Royle & Kery, 2007).

We used the Program MARK (White & Burnham, 1999) with species capture histories derived from multiple site visits within the two periods, 1993–1995 and 2011–2013. Capture histories for each species were constructed as encounter history vectors with fish detection (1), non-detection (0), or not surveyed (.) similar to mark–recapture studies (e.g., X_{ijt}; where X_{ijt} denotes the observed fish species occurrence status at visit j during period t to site i). Thus, the encounter history for a species at a site for which there were six overall sampling efforts might be denoted as 001.10. We expected misidentifications (false positives or false negatives) to be rare because the four study species are markedly different in appearance with slimy sculpin and longnose dace being the only benthic fish of their respective families within the basin. All species have well-known and easily identified distinguishing morphometric characteristics. These data were collected by trained field biologists with years of experience identifying fish in the basin. In addition, presence was determined by more than five individuals so a single or low level of misidentification should not influence the dataset.

Closure (or no occupancy state change) is required for the within period estimates of probability of detection (p) to accurately estimate occupancy, colonization and extirpation. We assessed the assumption of no occupancy state change (i.e., closure) within our time periods of 3 years using a staggered arrivals and departures approach described by Kendall, Hines, Nichols, and Grant (2013). For the within period estimates probability of detection (p), each site could have been visited up to six times, with 77% of the sites receiving at least two visits in period 1 and 78% of the sites receiving at least two visits in period 2.

We used a stepped approach to build models, first selecting the most supported detection probability model, then building models which incorporated detection efficiency to estimate initial site occupancy, extirpation, and finally colonization in consecutive order. First naive estimates for probability of detection were examined as a time varying function using the detection data to examine how different detection was within and across periods. Then we modeled a probability of detection function with the covariates for period, crew, gear type, and drainage area. We explored all possible combinations of these probability of detection covariates in competing models to determine those that best describe the probability of detection across sites (based on maximum likelihood estimates and Akaike information criterion [AIC] Arnold, 2010; Burnham & Anderson, 2002). We examined the naive estimates with the modeled estimates from our probability of detection function. Once the probability of detection function was parameterized, initial occupancy estimates for the first

period (1993–1995) were parameterized with the habitat covariates. We then estimated the extirpation and colonization probabilities that determined whether a species occurred at sites during the second sampling period, and whether those estimates were significantly different from zero. We considered all models within 2 AIC units of the top model, but disregarded uninformative parameters that were not statistically significant (see Supplemental Materials S2 for full model results). In the case where all other models were 2 AIC units or greater from the top model, we reported the second most supported model for comparison.

We validated the performance of top models by calculating the within-sample predictive performance of each model using a bootstrapped (1,000 times) formulation of area under the curve of the receiver operator characteristic plot (AUC; Fielding & Bell, 1997) and classification accuracy as performance metrics. AUC describes the ability of the model to discriminate between occupancy states (presence or absence), where an AUC value of 0.5 is no better than a random prediction and 1.0 indicates perfect discrimination. For cross-validation of the dynamic occupancy model, we compared model predictions for the second time period with a known occupancy state. Because one assumes a known occupancy state for cross-validation, we used sites surveyed during the second period (2011–2013) with at least three visits. This resulted in a cross-validation dataset of 92 sites in period 2 (2011–2013). Any three visits would result in a near perfect ($p > .98$) cumulative detection for all species.

Using the top occupancy models, we investigated how different scenarios of fragmentation may affect species distribution shifts. The models were used to predict first period (1993–1995) and second period (2011–2013) site occupancy under three scenarios (a) current conditions as parameterized in our top models, (b) if all barriers were ignored simulating free dispersal, and (c) if anthropogenic barriers were removed. We used a 1,000 time bootstrap sample of posterior distributions for the predictions. By ignoring all barriers, we estimated the influence of barriers within the model and how ignoring barriers in the modeling procedure might overestimate current distributions (and a species capacity to move upstream to thermal refuge sites). By removing anthropogenic barriers from the model, we explored the influence barrier management (either removal or facilitated dispersal) might have on species distributions.

3 | RESULTS

The 280 sample sites spanned a wide range of environmental conditions (Table 1). Between the two sample periods, a large portion of the basin experienced wildfires (Figure 1). In the initial period only 37 sites had burned in the two decades before sampling but in the later time period (2011–2013) 161 sites of the 280 sample sites were within wildfire perimeters. Three of the four species were distributed throughout streams in the river basin during the initial survey period (bull trout, cutthroat trout, and slimy sculpin), whereas longnose dace were generally detected along the main stem of the Bitterroot

TABLE 2 Detection probabilities for sampling events 1 (p1), event 2 (p2) ... and event 5 (p5) for four study species during the two closed periods (1993–1995, 2011–2013) based on naive (no covariates) time varying models. The sixth sampling event (p6) is not presented because detection probabilities are inestimable for that event. Standard errors are in parentheses

		Period 1 (1993–1995)					Period 2 (2011–2013)				
		p_1	p_2	p_3	p_4	p_5	p_1	p_2	p_3	p_4	p_5
Bull trout	Est (SE)	0.86 (0.03)	0.77 (0.03)	0.85 (0.05)	0.81 (0.06)	0.81 (0.04)	0.77 (0.08)	0.71 (0.07)	0.64 (0.06)	0.85 (0.11)	0.78 (0.09)
Westslope cutthroat trout	Est (SE)	0.94 (0.01)	0.87 (0.02)	0.89 (0.01)	0.87 (0.04)	0.90 (0.02)	0.97 (0.04)	0.92 (0.02)	0.85 (0.04)	0.97 (0.05)	0.93 (0.04)
Slimy sculpin	Est (SE)	0.86 (0.05)	0.84 (0.04)	0.80 (0.05)	0.82 (0.03)	0.80 (0.06)	0.88 (0.04)	0.88 (0.09)	0.87 (0.08)	0.90 (0.07)	0.89 (0.08)
Longnose dace	Est (SE)	0.87 (0.11)	0.91 (0.09)	0.84 (0.10)	0.92 (0.09)	0.88 (0.07)	0.94 (0.05)	0.93 (0.08)	0.89 (0.07)	0.93 (0.07)	0.88 (0.06)

TABLE 3 Dynamic occupancy models for fish species sampled at 280 sites across a riverscape over two sampling periods. The statistics are the number of parameters, K; change in Akaike's information criterion, ΔAIC; AIC weight, w; and the area under the cure (AUC) for each most supported model

Model	K	ΔAIC	w	AUC
Bull Trout[1]				
ψ(Barrier, Slope, Temp., Canopy Cover) ε(Slope, Temp.) γ(Temp.)	18	0.00	0.15	0.77
ψ(Barrier, Slope, Temp., Canopy Cover) ε(Slope, Temp.) γ(Temp., Burn Severity)	19	0.20	0.14	
ψ(Barrier, Slope, Temp., Canopy Cover) ε(Slope, Temp.) γ(Temp., Canopy Cover)	19	0.28	0.13	
ψ(Barrier, Slope, Temp., Canopy Cover) ε(Slope, Temp.) γ(Temp., Road Density)	19	1.50	0.07	
ψ(Barrier, Slope, Temp., Canopy Cover) ε(Slope, Temp.) γ(Temp, Basin Size)	19	1.58	0.07	
ψ(Barrier, Slope, Temp., Canopy Cover) ε(Slope, Temp.) γ(Temp, Barrier)	19	1.87	0.06	
[1]All bull trout models include time varying probability of detection (p1(Time) p2(Time))				
Westslope Cutthroat Trout[2]				
ψ(Barrier, Slope, Temp.) ε(.) γ(Barrier)	20	0.00	0.28	0.72
ψ(Barrier, Slope, Temp.) ε(.) γ(Barrier, Temp.)	21	1.34	0.14	
ψ(Barrier, Slope, Temp.) ε(.) γ(Barrier, Slope)	21	1.41	0.14	
ψ(Barrier, Slope, Temp.) ε(.) γ(.)	20	1.49	0.13	
ψ(Barrier, Slope, Temp.) ε(.) γ(Barrier, Canopy Cover)	21	1.93	0.11	
[2]All westslope cutthroat trout models include time varying probability of detection and basin size covariate (p1(Time, Basin Size) p2(Time, Basin Size))				
Slimy Sculpin[3]				
ψ(Barrier) ε(Temp., Burn Severity) γ(Barrier)	8	0.00	0.99	0.89
ψ(Barrier) ε(Temp., Burn Severity) γ(Burn Severity)	8	11.01	0.01	
Longnose Dace[3]				
ψ(Barrier, Temp.) ε(Temp.) γ(Barrier, Temp.)	9	0.00	0.96	0.70
ψ(Barrier, Temp.) ε(Temp.) γ(Barrier)	8	11.56	0.02	
[3]All models for slimy sculpin and longnose dace include constant probability of detection (p1(.) p2(.))				

Abbreviations: γ, colonization probability; ε, extirpation probability; ψ, initial occupancy probability; p1, probability of detection, period 1 (1993–1995); p2, probability of detection, period 2 (2011–2013).

TABLE 4 Parameter estimates of covariates in the top models for initial site occupancy, extirpation probability, and colonization probability of four fish species throughout a river network (standard error estimates are in parentheses). Non-significant covariates are left blank. Where ψ indicates initial occupancy probability, ε indicates extirpation probability, and γ represents colonization probability

Species	Parameter	Intercept	Barrier	Stream slope	Stream temperature	Burn severity	Canopy cover
Bull trout	ψ	0.46 (0.15)	−0.60 (0.18)	−0.46 (0.18)	−0.88 (0.21)		0.45 (0.17)
	ε	−1.55 (0.28)		0.70 (0.25)	1.36 (0.38)		
	γ	−1.94 (0.17)			−0.69 (0.31)		
Westslope cutthroat trout	ψ	3.33 (0.41)	−0.49 (0.15)	−0.54 (0.29)	−1.19 (0.37)		
	ε	−4.39 (0.62)					
	γ	−1.34 (0.31)	−0.94 (0.21)				
Slimy sculpin	ψ	−0.29 (0.24)	−2.35 (0.24)				
	ε	0.07 (0.22)			1.26 (0.24)	0.50 (0.17)	
	γ	−1.21 (1.09)	−2.21 (0.91)				
Longnose dace	ψ	−3.91 (0.55)	−1.27 (0.39)		1.86 (0.35)		
	ε	0.68 (1.05)			−3.31 (1.69)		
	γ	−1.38 (0.28)	−1.06 (0.54)		1.30 (0.38)		

TABLE 5 Estimates of occupancy, extirpation, and colonization probabilities for four fish species at 280 sample sites in the detection function from the top model from Table 3

	First period occupancy		Extirpation		Colonization		Second period occupancy[a]	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE
Bull trout	0.61	0.04	0.18	0.04	0.12	0.04	0.55	0.04
Westslope cutthroat trout	0.97	0.01	0.01	0.01	0.21	0.15	0.96	0.17
Slimy sculpin	0.43	0.06	0.57	0.06	0.02	0.02	0.19	0.04
Longnose dace	0.19	0.02	0.06	0.02	0.06	0.06	0.20	0.05

[a]Second period occupancy rate is derived from initial occupancy, extirpation, and colonization.

FIGURE 3 Raw observations for initially occupied sites where species persisted from 1993–1995 to 2011–2013 for (a) bull trout (green circles), (b) slimy sculpin (red circles), and (c) longnose dace (blue circles). Observed site extirpation (yellow triangles) and site colonization (orange squares) are also depicted

Bull trout   Slimy sculpin   Longnose dace
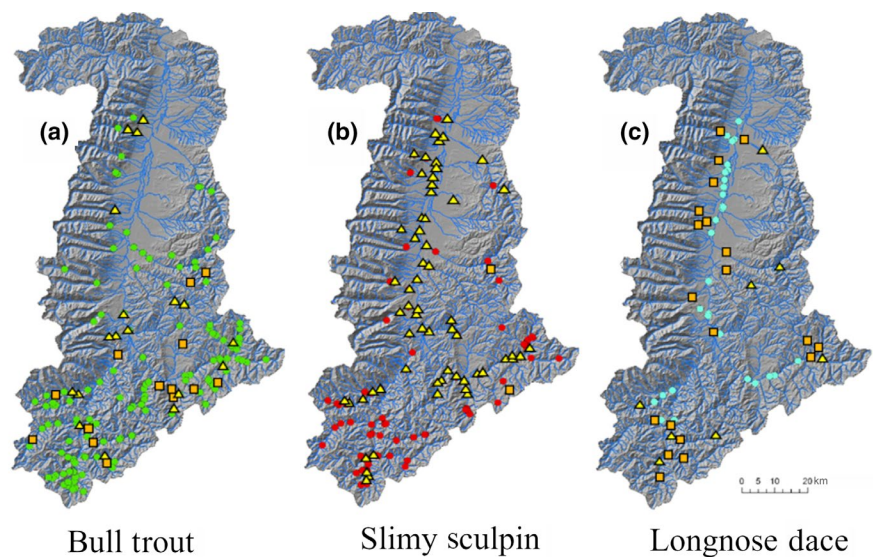
River and lower reaches of tributaries (Figure 2). Each of the four species had relatively high detection probabilities (slimy sculpin $p \geq .80$, longnose dace $p \geq .84$, westslope cutthroat trout $p \geq .80$, and bull trout $p \geq .64$) with the sampling protocol that was used. Naive detection probabilities by time were similar within sampling periods and between time periods among species (Table 2), highlighting that differences in detection probabilities were not driving the results in the dynamic occupancy models. In addition, conditional entry and
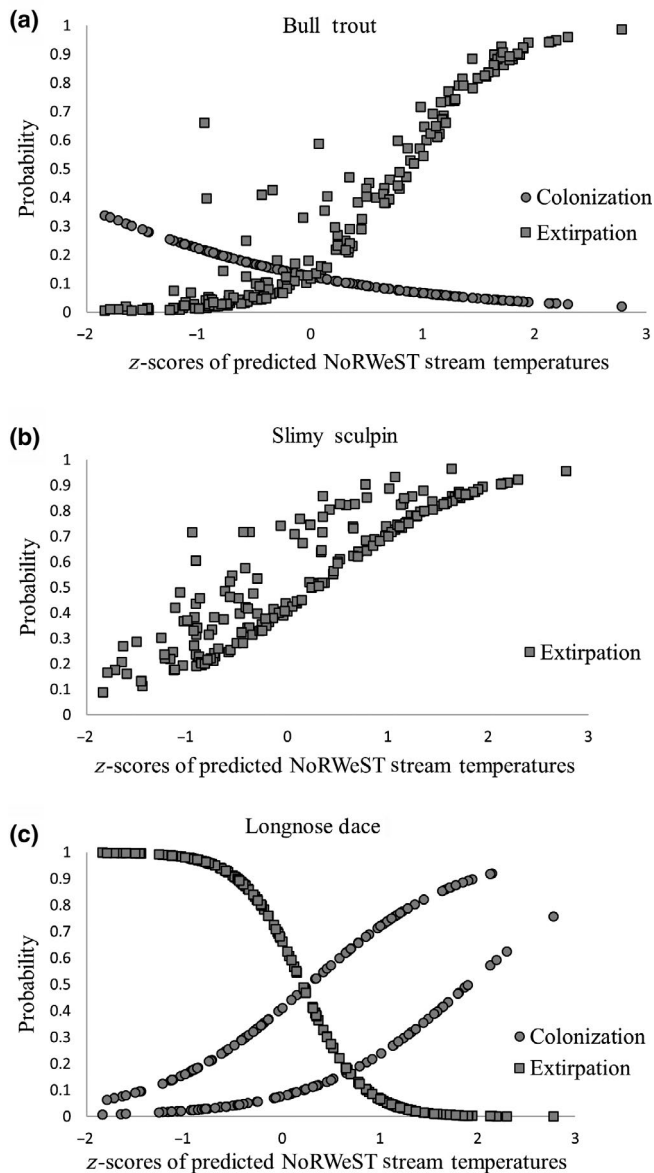
departure probabilities within our first time period (1993–1995) and within our defined second time period (2011–2013) were very low (<0.10) which supported our assumption of closure.

The covariates in the top models associated with probability of detection and initial occupancy varied by species, and all top models were well supported and made accurate predictions of second period occupancy (AUC 0.70–0.89; Table 3). Bull trout and westslope cutthroat trout had multiple models that fell within two AIC, but these models were similarly structured. The best models for bull trout and westslope cutthroat trout had time varying probabilities

FIGURE 4 Modeled probabilities of site extirpation and site colonization between sampling periods over a 20 year interval for (a) bull trout, (b) slimy sculpin, and (c) longnose dace. Colonization for slimy sculpin was rare. The bifurcation in modeled colonization probabilities for longnose dace is a result of landscape barriers strongly influencing colonization probabilities. Probabilities are illustrated across standardized z-score values for the range of mean August stream temperature in the 2011–2013 dataset
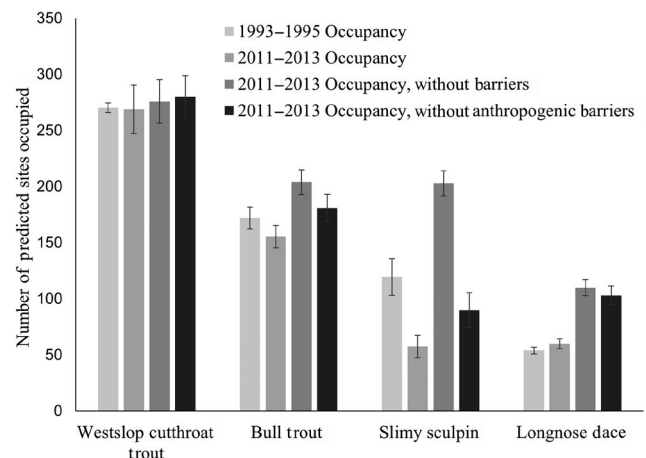
of detection; cutthroat trout detection probabilities were also influenced by drainage area. Slimy sculpin and longnose dace had strongly supported top models. The second most supported model was ΔAIC 11.01 for slimy sculpin and ΔAIC 11.56 for longnose dace from the top model. Detection probabilities for slimy sculpin and longnose dace were constant over time and were not influenced by habitat covariates or sampling gear or field crew. Initial site occupancy (ψ) of the two trout species was negatively associated with downstream barriers, and that were the warmest or highest gradient (steepest), with bull trout also positively associated with canopy cover. Slimy sculpin and longnose dace initial site occupancy was also negatively associated with downstream barriers (Table 4).

The different species had varying results in changes in occupancy during the study period. Bull trout site occupancy was estimated to have declined by 9.2% (95% confidence interval [CI] 8.3%–10.1%), from 200 sites in 53 streams in the initial period to 181 sites in 51 streams more recently (Table 5; Figure 3). Slimy sculpin estimated site occupancy declined by 48.0% (CI 42.0%–54.0%) between the two time periods, from 146 sites in 41 streams initially to 56 sites in 30 streams during the later survey period. Westslope cutthroat trout showed no significant change in site occupancy between time periods. Longnose dace was the only species that was observed to increase site occupancy during the study (42 sites in 24 streams during the first period, increasing to 55 sites in 26 streams during the second period).

Significant covariates describing site extirpation and colonization also varied among species. Site extirpation probabilities (ε) were positively associated with warmer stream temperatures for bull trout, warmer temperatures and wildfire occurrence for slimy sculpin, and cooler temperatures for longnose dace (Tables 3 and 4). Extirpation probability for westslope cutthroat trout was very low over this time period. Site colonization probabilities (γ) among the four species were consistently affected by temperature and barriers, although several other factors appeared in closely competing models for

FIGURE 5 Predicted sites occupied in the second time period (2011–2013) with barriers, without barriers and without anthropogenic barriers with 95% confidence intervals based on 1,000 iteration bootstrapping. Landscape barriers impact weak-swimming fishes more so than strong-swimming fishes

the two trout species (Table 3). Parameter estimates from the top models reinforce the important roles that stream temperature and barriers played in site occupancy and turnover (Table 4). Whereas barriers had a consistently negative effect on species occurrence and colonization, temperature effects varied by species. Bull trout and slimy sculpin showed significant higher extirpation probabilities and lower colonization probabilities for bull trout only at warmer sites and slimy sculpin had no measurable colonization while longnose dace demonstrated the opposite trend (Figure 4; Figures S2 and S3). Bull trout extirpation and colonization probabilities intersected at a mean temperature z-score of 0.05, which translated to a mean August temperature of 12.1°C. Bull trout and slimy sculpin had 50% extirpation probabilities at z-scores of 0.79 and 0.23, which translated to mean August temperatures of 12.8°C and 11.5°C, respectively. Slimy sculpin extirpation probabilities were high overall and much higher in higher order, warmer streams and streams that had moderate to severe wildfires between time periods (Figure 4). Westslope cutthroat trout did not have any significant temperature relationships.

Barrier removal scenarios suggested different levels of species sensitivity (Figure 5). Removal of all barriers indicated slimy sculpin could occupy a much broader set of sites compared to those recently occupied in the 2011–2013 period. Even if only anthropogenic barriers were addressed and natural barriers remained, a substantial increase of 22% in the number of sites occupied by sculpin appeared possible. Most of the barriers influencing longnose dace colonization between time periods were anthropogenic barriers, but if these structures were passable it was estimated that site occupancy could increase by 80%. Given the broad initial distribution of the two trout species, their potential site occupancy was less affected by barrier removal. Bull trout sites occupied might increase by 16% with anthropogenic barrier removal, whereas cutthroat trout gains were estimated to be negligible.

4 | DISCUSSION

Our results highlight the unique responses that individual species exhibit within a diverse riverscape over two decades. Depending on the species, their distributions contracted, expanded, or remained constant, with specific response emerging from the interplay among species traits, initial distributions, fluvial access to new habitats, and location (e.g., closeness to thermal threshold). The two trout species that were initially distributed throughout the network, including the upper, colder landscape showed little change, although small contractions in warmer habitats were observed for bull trout. The vagility of these species enabled habitat tracking and likely enhanced their resilience to the extensive wildfires that occurred between the first period (1993–1995) and second period of the study (2011–2013). Trends for the two smaller species appeared to be on diverging trajectories and differed from that of the trout species. Slimy sculpin exhibited a surprising loss in occupancy of the 20 years, which seemed to be driven by climate change and landscape

resistance. Longnose dace with a preference for warmer temperatures, was mostly distributed in the lowest elevation and warmest stream sites in and along the Bitterroot River that had little exposure to wildfires. Longnose dace did initially occupy some upper elevation sites ($n = 6$) but this was generally by low numbers of fish (5–10 or 0.01–0.1 fish/m) and these sites were surrounded by unoccupied sites suggesting these fish were at low densities and patchy at these higher elevations. Dace were extirpated at these sites by the second period. Some sites did have fire present but given the few number of sites it is difficult to assess whether these extirpations were stochastic events or driven by environmental conditions. Wildfires are common to landscapes in western North America where these four species evolved, but instream habitats are often degraded for several years postfire such that local temporary refuges may be periodically necessary, as well as dispersal or recolonization from nearby refuges or populations may be needed. Recolonization of some sites could eventually occur but the lower vagility of sculpin and dace likely make it a longer process than is likely for trout species which often rebound to prefire abundances within a few years after fires (reviewed in Bixby et al., 2015).

Conservation concerns are likely to vary by species during the remainder of the century. Climate change within this region is projected to continue along trends that have been ongoing for several decades, with additional stream temperature increases of 1–2°C, summer flow declines of 20%–40%, and more frequent wildfires over the course of the 21st century (e.g., Isaak, Wenger, Peterson, et al., 2017; Leppi et al., 2012; Westerling, Hidalgo, Cayan, & Swetnam, 2006). Longnose dace seem poised to emerge as a possible climate winner in the future but their colonization into new habitats may be compromised by habitat fragmentation in some areas, as we detected significant negative effects of anthropogenic barriers on colonization probabilities in currently suitable reaches in the Bitterroot valley. The effect of small barriers negatively impacting longnose dace movement is consistent with work highlighting their inability to pass stream barriers (Ficke, 2015; Ficke & Myrick, 2019). Future predatory invaders that prefer warmer temperatures and riverine habitats may also pose a risk to longnose dace and other small-bodied members of the aquatic community. For example, a nonnative brown trout (*Salmo trutta*) population has recently been expanding in the Bitterroot River (Al-Chokhachy et al., 2016), and smallmouth bass (*Micropterus dolomieu*) are undergoing a regional expansion and prefer the same warmer, low velocity habitats that longnose dace inhabit (Rubenson & Olden, 2019). Those warmer habitats may also be vulnerable to non-predatory species invasions that alter aquatic ecosystems in deleterious ways through various trophic pathways (e.g., Messager & Olden, 2018). The lack of change in westslope cutthroat trout distributions we observed was similar to the results of an earlier study with the Yellowstone cutthroat trout (*O. clarki bouvieri*) subspecies which resampled historical sites throughout a river network (Meyer, Schill, Elle, & Schrader, 2003). Given the historical unknown levels of introgression with congeneric rainbow trout, our analysis could not detect any potential expansion of low levels of introgression with rainbow

trout as seen in other Montana river basins in Montana (Boyer, Muhlfeld, & Allendorf, 2008; Muhlfeld et al., 2014). Even though historical changes in westslope cutthroat trout did not occur in this study, there have been projections for future climate-related range contractions for westslope cutthroat trout in this region (Isaak et al., 2015; Williams, Haak, Neville, & Colyer, 2009) but larger changes may be necessary for these to manifest.

The conservation needs of the two declining species, bull trout and slimy sculpin, are more challenging. For bull trout, our results were similar to previous descriptions of thermal preferences being <12°C (Isaak et al., 2016) and reinforce previous trend assessments and the role that climate change appears to be playing in slow ongoing, patchy declines throughout this basin and the broader region (Al-Chokhachy et al., 2016; Eby et al., 2014). Our ability to estimate thermal constraints based on extirpation and colonization probabilities suggests that site turnover is equal at 12.1°C. However, the particularly cold thermal niche of bull trout restricts most of their site occurrences and reproductive areas to headwater habitats where climate velocities are slower (Isaak et al., 2016). Motivated by these factors, previous research developed precise species distribution models to forecast the locations of streams that may act as long-term climate refugia for populations of this species (Isaak et al., 2015; Young et al., 2016). Several of these predicted refugia occur within the Bitterroot watershed and may serve as the focus of conservation efforts to minimize the loss of life history diversity (Nyce, Eby, Clancy, Painter, & Leary, 2013), reduce invasions by nonnative competitors (Wilcox et al., 2018), and improve habitat quality.

The magnitude of slimy sculpin declines during the study was most surprising and noteworthy. These losses are not isolated to this basin, as Adams et al. (2015) detected temperature-dependent changes in distributions occurring from 13°C to 16°C in other basins in Montana with warming stream temperatures that were not exposed to wildfire. We observed lower mean August temperatures (11.8°C) associated with 50% extirpation probability, yet there is likely a difference between mean estimates of temperature and direct measures of temperature. Moreover, relatively little is known about the population dynamics and spatial ecology of this species due to a lack of historical monitoring in many areas throughout its range. So little attention has been focused on sculpin species in general that their phylogeography in western North America is currently undergoing a revision (M. K. Young, personal communication, November 2013) and recent studies have revealed cryptic biodiversity that remains underappreciated (Adams & Schmetterling, 2007; LeMoine et al., 2014; Young, McKelvey, Pilgrim, & Schwartz, 2013). The direct causes of decline are uncertain, even though the association with stream temperature is strong, there could be additional considerations such as species interactions (Baltz, Moyle, & Knight, 1982). Slimy sculpin populations warrant broader monitoring to understand future population trajectories, a broader review of their status, their potential cause of declines, and a formal consideration into potential conservation interventions, such as improving passage at barriers for weak-swimming fish.

The range of distributional responses and potential vulnerabilities among the four study species was notable but likely provides an underestimate of changes in aquatic biodiversity of the broader riverscape. Many additional nongame fish (in cyprinidae or catostomidae families) often have little information on their occurrence or abundance, but given their morphology, they are likely also impacted by barriers limiting colonization upstream. As we work to understand the broader biodiversity changes from macroinvertebrates, mussels, amphibians and the full assemblage of fishes, surveys that efficiently capture the environmental DNA of organisms transported downstream through river networks (Deiner, Fronhofer, Mächler, Walser, & Altermatt, 2016) could help develop more comprehensive information. These data could then be used to screen for vulnerable species and to identify locally important biodiversity hotspots that could guide conservation investments (Kalinkat et al., 2017).

Even though the importance of addressing barriers to dispersal has been described for species climate resilience (Parmesan et al., 1999) and associated with climate vulnerability of freshwater fishes (Comte & Grenouillet, 2013; Gibson-Reinemer, Rahel, Albeke, & Fitzpatrick, 2017; Hari et al., 2006; Nyboer, Liang, & Chapman, 2019), our study is rare in its ability to estimate effects on barriers with the demonstration of how they may have already impacted small fish's ability to respond to changes in stream temperature. As biologists work to incorporate barriers into projections and planning (e.g., Pandit, Maitland, Pandit, Poesch, & Enders, 2017), detailed and species-specific inventories of barriers to movements of all freshwater organisms will be needed to complement species distribution information and inform future responses to climate change (Hari et al., 2006; Januchowsky-Hartley, Jezequel, & Tedesco, 2019). As our results illustrate, barriers are common even throughout a sparsely populated watershed such as the Bitterroot basin and appear to impact species ability to respond to changes in stream temperatures and wildfire disturbances. Although the deleterious effects of habitat fragmentation and the ease with which connectivity in dendritic river networks can be severed have long been recognized (e.g., Zwick, 1992), only recently has the pervasiveness of barrier features and their influence on climate vulnerability been appreciated (e.g., Gibson-Reinemer et al., 2017; Januchowsky-Hartley et al., 2019; Radinger et al., 2017; Radinger, Holker, Horky, Slavik, & Wolter, 2018). Most commonly available information about barrier locations is limited to summaries of the largest anthropogenic features such as dams and major water diversions found in national dam inventories. Passage considerations at many of those larger barriers are focused on strong-swimming fish such as salmonids, and are likely ineffective for most other species (Birnie-Gauvin, Franklin, Wilkes, & Aarestrup, 2019; Januchowsky-Hartley et al., 2019). Information about the locations of smaller anthropogenic barriers such as check dams for small irrigation diversions are often held by local water resource agencies, which may or may not be publicly available for use in research, and is often lacking with regards to aquatic organism passage details. Similarly with regards to

natural barriers, usually only the most prominent features like waterfalls on larger rivers are well catalogued despite being common in smaller mountain headwater streams where reaches with steep slopes also create numerous flow velocity barriers for aquatic organisms. Identifying these barriers and including them in distribution modeling is key for better assessing risks to individual species and community integrity while improving conservation planning to increase riverscape resilience (Januchowsky-Hartley et al., 2019).

Despite significant challenges, numerous actions could be taken that would improve the resilience of aquatic communities to environmental change. Habitat restoration measures designed to regain the attributes of more natural thermal or hydrologic regimes where alterations are significant could offset many past and future effects of climate change (e.g., Justice, White, McCullough, Graves, & Blanchard, 2017). Barrier removal, or provision of better fish passage facilities, is an obvious measure. Significant progress has been made on this front for cold-water species in headwater tributaries where road crossings are sometimes problematic but smaller-bodied fish have received less attention. Attempts to improve fluvial connectivity, however, must also be weighed against possible risks associated with facilitating the movements of invasive species, predators, or diseases (Fausch, Rieman, Dunham, Young, & Peterson, 2009). Some considerations may be assisted migration via human-mediated transfer of species over upstream barriers into suitable habitats or selective passage to promote native species passage and inhibit non-native fish (Rahel & McLaughlin, 2018). Suppression of undesired and invasive species is another tactic but one that is notoriously difficult and has been met with mixed success (e.g, Britton, Gozlam, & Copp, 2011; Meronek et al., 1996).

5 | CONCLUSION

By revisiting hundreds of historical sites across a complex riverscape, this study establishes important empirical benchmarks for future comparisons and hints at the breadth of ecological responses occurring in aquatic communities subject to climate change and related disturbances. It appears that communities are not simply shifting *en masse* to track suitable habitats but are being disrupted by the varying degrees of landscape resistance that community members experience. Two smaller-bodied, less vagile species demonstrated responses that were distinct from larger-bodied, cold-water salmonid species that inhabit different portions of the same river network. This study highlights that although salmonid species have been the primary focus of the literature concerning climate vulnerability in North America (e.g., Eby et al., 2014; Wenger et al., 2011), they were not the most vulnerable species in this analysis. Better information is needed to understand the distribution, habitat requirements, mobility, and dispersal capabilities of many lesser-known species so that changes underway in freshwater ecosystems are described more comprehensively and efficient conservation strategies can be designed accordingly. An incomplete knowledge of the locations and extent of anthropogenic and natural barriers to aquatic organism movements within riverscapes could undermine those conservation efforts by preventing species from tracking shifts in suitable habitats. Local barrier inventories may be useful for identifying where constraints are most likely to occur and prioritizing efforts to improve aquatic organism passage or assisted migrations in conjunction with habitat improvement efforts that enhance community resilience. Concerted efforts will be required to conserve biodiversity within freshwater environments this century as anthropogenic climate change continues for the foreseeable future.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available in the supplementary material of this article or can be made available from the corresponding author upon reasonable request.

ORCID
Michael T. LeMoine https://orcid.org/0000-0003-3605-7335

REFERENCES
Adams, S., & Schmetterling, D. (2007). Freshwater sculpins: Phylogenetics to ecology. *Transactions of the American Fisheries Society*, *136*(6), 1736–1741. https://doi.org/10.1577/T07-023.1

Adams, S., Schmetterling, D., & Neely, D. (2015). Summer stream temperatures influence sculpin distributions and spatial partitioning in the upper clark fork river basin, Montana. *Copeia*, *103*(2), 416–428. https://doi.org/10.1643/CE-14-229

Albanese, B., Angermeier, P., & Peterson, J. (2009). Does mobility explain variation in colonization and population recovery among stream fishes? *Freshwater Biology*, *54*(7), 1444–1460.

Al-Chokhachy, R., Schmetterling, D., Clancy, C., Saffel, P., Kovach, R., Nyce, L., ... Pierce, R. (2016). Are brown trout replacing or displacing bull trout populations in a changing climate? *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(9), 1395–1404. https://doi.org/10.1139/cjfas-2015-0293

Alofs, K., Jackson, D., & Lester, N. (2014). Ontario freshwater fishes demonstrate differing range-boundary shirts in a warming climate. *Diversity and Distributions*, *20*, 123–136.

Altermatt, F. (2013). Diversity in riverine metacommunities: A network perspective. *Aquatic Ecology*, *47*, 365–377. https://doi.org/10.1007/s10452-013-9450-3

Angert, A., Crozier, L., Rissle, L., Gilman, S., Tewksbury, J., & Chunco, A. (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, *14*(7), 677–689. https://doi.org/10.1111/j.1461-0248.2011.01620.x

Arnold, C., & Gibbons, C. (1996). Impervious surface coverage: The emergence of a key environmental indicator. *Journal of the American Planning Association*, *62*, 243–258. https://doi.org/10.1080/01944369608975688

Arnold, T. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management*, 74, 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Bálint, M., Domisch, S., Engelhardt, C., Haase, P., Lehrian, S., Sauer, J., … Nowak, C. (2011). Cryptic biodiversity loss linked to global climate change. *Nature Climate Change*, 1(6), 313–318. https://doi.org/10.1038/nclimate1191

Baltz, D. M., Moyle, P. B., & Knight, N. J. (1982). Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 1502–1511.

Bear, E., McMahon, T., & Zale, A. (2007). Comparative thermal requirements of westslope cutthroat trout and rainbow trout: Implications for species interactions and development of thermal protection standards. *Transactions of the American Fisheries Society*, 136(4), 1113–1121. https://doi.org/10.1577/T06-072.1

Behlke, C., Kane, D., McLean, R., & Travis, M. (1991). *Fundamentals of culvert design for passage of weak-swimming fish*. USA: Alaska Department of Fish and Game. Retrieved from http://www.dot.state.ak.us/stwddes/research/assets/pdf/fhwa_ak_rd_90_10.pdf

Bell, M., Delacy, A., Paulik, G., Bruya, K., & Scott, C. (1981). *Updated compendium on the success of passage of small fish through turbines* (pp. 1–25). Portland, OR: Report to U.S. Army Corps of Engineers. Contract DACW-6P-76-C-0254.

Birnie-Gauvin, K., Franklin, P., Wilkes, M., & Aarestrup, K. (2019). Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(7), 1095–1105.

Bixby, R., Cooper, S., Gresswell, R., Brown, L., Dahm, C., & Dwire, K. (2015). Fire effects on aquatic ecosystems: An assessment of the current state of the science. *Freshwater Science*, 34(4), 1340–1350. https://doi.org/10.1086/684073

Boyer, M., Muhlfeld, C., & Allendorf, F. (2008). Rainbow trout (*Oncorhynchus mykiss*) invasion and the spread of hybridization with native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). *Canadian Journal of Fisheries and Aquatic Sciences*, 65(4), 658–669.

Britton, J., Gozlam, R., & Copp, G. (2011). Managing non-native fish in the environment. *Fish and Fisheries*, 12, 256–274. https://doi.org/10.1111/j.1467-2979.2010.00390.x

Buisson, L., Thuiller, W., Lek, S., Lim, P., & Grenouillet, G. (2008). Climate change hastens the turnover of stream fish assemblages. *Global Change Biology*, 14(10), 2232–2248. https://doi.org/10.1111/j.1365-2486.2008.01657.x

Burnham, K., & Anderson, D. (2002). *Model selection and multimodel inference: A practical information–theoretic approach*. New York, NY: Springer-Verlag.

Burton, T. (2005). Fish and stream habitat risks from uncharacteristic wildfire: Observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. *Forest Ecology and Management*, 211(1–2), 140–149. https://doi.org/10.1016/j.foreco.2005.02.063

Carroll, C., Parks, S., Dobrowski, S., & Roberts, D. (2018). Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America. *Global Change Biology*, 24(11), 5318–5331. https://doi.org/10.1111/gcb.14373

Chen, I., Hill, J., Ohlemuller, R., Roy, D., & Thomas, C. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026. https://doi.org/10.1126/science.1206432

Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshwater Biology*, 58(4), 625–639. https://doi.org/10.1111/fwb.12081

Comte, L., & Grenouillet, G. (2013). Do stream fish track climate change? Assessing distribution shifts in recent decades across France. *Ecography*, 36, 1236–1246. https://doi.org/10.1111/j.1600-0587.2013.00282.x

Comte, L., Murienne, J., & Grenouillet, G. (2014). Species traits and phylogenetic conservatism of climate-induced range shifts in stream fishes. *Nature Communications*, 5, 5053. https://doi.org/10.1038/ncomms6053

Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Deiner, K., Fronhofer, E., Mächler, E., Walser, J., & Altermatt, F. (2016). Environmental DNA reveals that rivers are conveyer belts of biodiversity information. *Nature Communications*, 7, 12544. https://doi.org/10.1038/ncomms12544

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dudgeon, D., Arthington, A., Gessner, M., Kawabata, Z., Knowler, D., Lévêque, C., … Sullivan, C. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81(2), 163–182. https://doi.org/10.1017/S1464793105006950

Eby, L., Helmy, O., Holsinger, L., & Young, M. (2014). Evidence of climate-induced range contractions in bull trout *Salvelinus confluentus* in a Rocky Mountain Watershed, U.S.A. *PLoS One*, 9(6), e98912. https://doi.org/10.1371/journal.pone.0098812

Fausch, K., Rieman, B., Dunham, J., Young, M., & Peterson, D. (2009). Invasion versus isolation: Trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology*, 23(4), 859–870. https://doi.org/10.1111/j.1523-1739.2008.01159.x

Ficke, A. D. (2015). Mitigation measures for barriers to Great Plains fish migration. PhD dissertation, Colorado State University; pdf available via Google Scholar.

Ficke, A. D., & Myrick, C. A. (2019). A method for monitoring movements of small fishes in urban streams. *North American Journal of Fisheries Management*, 29, 1444–1453. https://doi.org/10.1577/m08-248.1

Fielding, A., & Bell, J. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24, 38–49. https://doi.org/10.1017/S0376892997000088

Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vié, J.-C., Akçakaya, H. R., Angulo, A., … Mace, G. M. (2013). Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. *PLoS One*, 8(6), e65427. https://doi.org/10.1371/journal.pone.0065427

Fraley, J., & Shepard, B. (1989). Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system. *Northwest Science*, 63(4), 133–143.

Gibson-Reinemer, D., Rahel, F., Albeke, S., & Fitzpatrick, R. (2017). Natural and anthropogenic barriers to climate tracking in river fishes along a mountain–plains transition zone. *Diversity and Distributions*, 23(7), 761–770. https://doi.org/10.1111/ddi.12576

Grinnell, J., & Storer, T. (1924). *Animal life in the Yosemite*. Berkeley, CA: University of California Press.

Haidvogl, G., Lajus, D., Pont, D., Schmid, M., Jungwirth, M., & Lajus, J. (2014). Typology of historical sources and the reconstruction of long-term historical changes of riverine fish: A case study of the Austrian Danube and northern Russian rivers. *Ecology of Freshwater Fish*, 23(4), 498–515. https://doi.org/10.1111/eff.12103

Hamlet, A., Mote, P., Clark, M., & Lettenmaier, D. (2007). Twentieth-century trends in runoff, evapotranspiration, and soil moisture in the western United States. *Journal of Climate*, 20(8), 1468–1486. https://doi.org/10.1175/JCLI4051.1

Hari, R., Livingstone, D., Siber, R., Burkhardt-Holm, P., & Guettinger, H. (2006). Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams. *Global Change Biology*, 12(1), 10–26. https://doi.org/10.1111/j.1365-2486.2005.001051.x

Harrell, F. E., Lee, K. L., Califf, R. M., Pryor, D. B., & Rosati, R. A. (1984). Regression modelling strategies for improved prognostic prediction. *Statistics in Medicine*, 3(2), 143–152. https://doi.org/10.1002/sim.4780030207

Hawkins, C., Kershner, J., Bisson, P., Bryant, M., Decker, L., Gregory, S., … Young, M. (1993). A hierarchical approach to classifying stream habitat features. *Fisheries*, 18(6), 3–12.

Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: Detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, 84(1), 39–54. https://doi.org/10.1111/j.1469-185X.2008.00060.x

Hijmans, R., Cameron, S., Parra, J., Jones, P., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978. https://doi.org/10.1002/joc.1276

Holsinger, L., Keane, R., Isaak, D., Eby, L., & Young, M. (2014). Relative effects of climate change and wildfires on stream temperatures: A simulation modeling approach in a Rocky Mountain watershed. *Climatic Change*, 124(1–2), 191–206. https://doi.org/10.1007/s10584-014-1092-5

Howell, P., Dunham, J., & Sankovich, P. (2010). Relationships between water temperatures and upstream migration, cold water refuge use, and spawning of adult bull trout from the Lostine River, Oregon, USA. *Ecology of Freshwater Fish*, 19(1), 96–106. https://doi.org/10.1111/j.1600-0633.2009.00393.x

Isaak, D., Luce, C., Horan, D., Chandler, G., Wollrab, S., & Nagel, D. (2018). Global warming of salmon and trout rivers in the Northwestern US: Road to ruin or path through purgatory? *Transactions of the American Fisheries Society*, 147(3), 566–587. https://doi.org/10.1002/tafs.10059

Isaak, D., Luce, C., Rieman, B., Nagel, D., Peterson, E., Horan, D., … Chandler, G. (2010). Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications*, 20(5), 1350–1371. https://doi.org/10.1890/09-0822.1

Isaak, D. J., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Nagel, D. E., Luce, C. H., … Parkes-Payne, S. (2017). The NorWeST summer stream temperature model and scenarios for the western US: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. *Water Resources Research*, 53(11), 9181–9205. https://doi.org/10.1002/2017WR020969

Isaak, D. J., Wenger, S. J., & Young, M. K. (2017). Big biology meets microclimatology: Defining thermal niches of ectotherms at landscape scales for conservation planning. *Ecological Applications*, 27(3), 977–990. https://doi.org/10.1002/eap.1501

Isaak, D., Young, M., Luce, C., Hostetler, S., Wenger, S., Peterson, E., … Nagel, D. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 113(16), 4374–4379. https://doi.org/10.1073/pnas.1522429113

Isaak, D. J., Young, M. K., Nagel, D. E., Horan, D. L., & Groce, M. C. (2015). The cold-water climate shield: Delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology*, 21(7), 2540–2553. https://doi.org/10.1111/gcb.12879

Januchowsky-Hartley, S. R., Jezequel, C., & Tedesco, P. A. (2019). Modelling built infrastructure heights to evaluate common assumptions in aquatic conservation. *Journal of Environmental Management*, 232(2019), 131–137.

Justice, C., White, S., McCullough, D., Graves, D., & Blanchard, M. (2017). Can stream and riparian restoration offset climate change impacts to salmon populations? *Journal of Environmental Management*, 188, 212–227. https://doi.org/10.1016/j.jenvman.2016.12.005

Kalinkat, G., Cabral, J. S., Darwall, W., Ficetola, G. F., Fisher, J. L., Giling, D. P., … Jarić, I. (2017). Flagship umbrella species needed for the conservation of overlooked aquatic biodiversity. *Conservation Biology*, 31(2), 481–485. https://doi.org/10.1111/cobi.12813

Kendall, W., Hines, J., Nichols, J., & Grant, E. (2013). Relaxing the closure assumption in occupancy models: Staggered arrival and departure times. *Ecology*, 94(3), 610–617. https://doi.org/10.1890/12-1720.1

LeMoine, M., & Bodensteiner, L. (2014). Barriers to upstream passage by two migratory sculpins, prickly sculpin (*Cottus asper*) and coastrange sculpin (*Cottus aleuticus*), in northern Puget Sound lowland streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(11), 1758–1765.

LeMoine, M., Young, M., McKelvey, K., Eby, L., Pilgrim, K., & Schwartz, M. (2014). *Cottus schitsuumsh*, a new species of sculpin (Scorpaeniformes: Cottidae) in the Columbia River basin, Idaho-Montana, USA. *Zootaxa*, 3755(3), 241–258.

Lenoir, J., Gégout, J., Marquet, P., De Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884), 1768–1771.

Leppi, J., DeLuca, T., Harrar, S., & Running, S. (2012). Impacts of climate change on August stream discharge in the Central-Rocky Mountains. *Climatic Change*, 112(3–4), 997–1014. https://doi.org/10.1007/s10584-011-0235-1

Littell, J., Elsner, M., Mauger, G., Lutz, E., Hamlet, A., & Salathé, E. (2011). Regional climate and hydrologic change in the northern US Rockies and Pacific Northwest: Internally consistent projections of future climate for resource management. Retrieved from http://cses.washington.edu/picea/USFS/pub/Littell_etal_2010/Littell_etal._2011_Regional_Climatic_And_Hydrologic_Change_USFS_USFWS_JVA_17Apr11.pdf

Luce, C., & Holden, Z. (2009). Declining annual streamflow distributions in the Pacific Northwest United States, 1948–2006. *Geophysical Research Letters*, 36(16), 1948–2006. https://doi.org/10.1029/2009GL039407

Lynch, A., Myers, B., Chu, C., Eby, L., Falke, J., Kovach, R., … Whitney, J. (2016). Climate change effects on North American inland fish populations and assemblages. *Fisheries*, 41(7), 346–361. https://doi.org/10.1080/03632415.2016.1186016

Lyons, J., Zorn, T., Stewart, J., Seelbach, P., Wehrly, K., & Wang, L. (2009). Defining and characterizing coolwater streams and their fish assemblages in Michigan and Wisconsin, USA. *North American Journal of Fisheries Management*, 29, 1130–1151. https://doi.org/10.1577/M08-118.1

MacKenzie, D., Nichols, J., Hines, J., Knutson, M., & Franklin, A. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, 84(8), 2200–2207. https://doi.org/10.1890/02-3090

MacLean, S., & Beissinger, S. (2017). Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Global Change Biology*, 23(10), 4094–4105. https://doi.org/10.1111/gcb.13736

Mahlum, S., Eby, L., Young, M., Clancy, C., & Jakober, M. (2011). Effects of wildfire on stream temperatures in the Bitterroot River Basin, Montana. *International Journal of Wildland Fire*, 20(2), 240–247. https://doi.org/10.1071/WF09132

Mawdsley, J., O'Malley, R., & Ojima, D. (2009). A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conservation Biology*, 23(5), 1080–1089. https://doi.org/10.1111/j.1523-1739.2009.01264.x

McGuire, J., Lawler, J., McRae, B., Nuñez, T., & Theobald, D. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences of the United States of America*, 113(26), 7195–7200. https://doi.org/10.1073/pnas.1602817113

Meronek, T., Bouchard, P., Buckner, E., Burri, T., Demmerly, K., Hatleli, D., … Coble, D. (1996). A review of fish control projects. *North American Journal of Fisheries Management*, 16, 63–74. https://doi.org/10.1577/1548-8675(1996)016<0063:AROFCP>2.3.CO;2

Messager, M., & Olden, J. (2018). Individual-based models forecast the spread and inform the management of an emerging riverine invader. *Diversity and Distributions*, 24(12), 1816–1829. https://doi.org/10.1111/ddi.12829

Meyer, K., Schill, D., Elle, F., & Schrader, W. (2003). A long-term comparison of Yellowstone cutthroat trout abundance and size structure in their historical range in Idaho. *North American Journal of Fisheries Management*, 23, 149–162. https://doi.org/10.1577/1548-8675(2003)023<0149:ALTCOY>2.0.CO;2

Millar, C., Westfall, R., Delany, D., King, J., & Graumlich, J. (2004). Response of subalpine conifers in the Sierra Nevada, California, USA, to 20th-century warming and decadal climate variability. *Arctic, Antarctic, and Alpine Research*, 36(2), 181–200. https://doi.org/10.1657/1523-0430(2004)036[0181:ROSCIT]2.0.CO;2

Morgan, P., Hardy, C., Swetnam, T., Rollins, M., & Long, D. (2001). Mapping fire regimes across time and space: Understanding coarse and fine-scale fire patterns. *International Journal of Wildland Fire*, 10(4), 329–342. https://doi.org/10.1071/WF01032

Moritz, C., Patton, J., Conroy, C., Parra, J., White, G., & Beissinger, S. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, 322(5899), 261–264.

Mote, P. W., Li, S., Lettenmaier, D. P., Xiao, M., & Engel, R. (2018). Dramatic declines in snowpack in the western US. *npj Climate and Atmospheric Science*, 1(1), 1–6. https://doi.org/10.1038/s41612-018-0012-1

Muhlfeld, C., Kovach, R., Jones, L., Al-Chokhachy, R., Boyer, M., Leary, R., ... Allendorf, F. (2014). Invasive hybridization in a threatened species is accelerated by climate change. *Nature Climate Change*, 4(7), 620. https://doi.org/10.1038/nclimate2252

Nislow, K., Hudy, M., Letcher, B., & Smith, E. (2011). Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: Implications for management and conservation. *Freshwater Biology*, 56(10), 2135–2144. https://doi.org/10.1111/j.1365-2427.2011.02634.x

Nyboer, E. A., Liang, C., & Chapman, L. J. (2019). Assessing the vulnerability of Africa's freshwater fishes to climate change: A continent-wide trait-based analysis. *Biological Conservation*, 236, 505–520. https://doi.org/10.1016/j.biocon.2019.05.003

Nyce, L., Eby, L., Clancy, C., Painter, S., & Leary, F. (2013). Genetic population structure of bull trout in the East Fork Bitterroot River drainage, Montana. *North American Journal of Fisheries Management*, 33(2), 432–445. https://doi.org/10.1080/02755947.2013.768565

Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., ... Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, 5(3), 215. https://doi.org/10.1038/nclimate2448

Pandit, S. N., Maitland, B. M., Pandit, L. K., Poesch, M. S., & Enders, E. C. (2017). Climate change risks, extinction debt, and conservation implications for a threatened freshwater fish: Carmine shiner (Notropis percobromus). *Science of The Total Environment*, 598, 1–11. https://doi.org/10.1016/j.scitotenv.2017.03.228

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J., Thomas, C., Descimon, H., & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399(6736), 579–583.

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37–42.

Pederson, G., Graumlich, L., Fagre, D., Kipfer, T., & Muhlfeld, C. (2010). A century of climate and ecosystem change in Western Montana: What do temperature trends portend? *Climatic Change*, 98, 133–154. https://doi.org/10.1007/s10584-009-9642-y

Popescu, V., De Valpine, P., Tempel, D., & Peery, M. (2012). Estimating population impacts via dynamic occupancy analysis of Before–After Control–Impact studies. *Ecological Applications*, 22(4), 1389–1404. https://doi.org/10.1890/11-1669.1

Potter, K., Woods, H., & Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global Change Biology*, 19, 2932–2939.

Radinger, J., Essl, F., Hölker, F., Horký, P., Slavík, O., & Wolter, C. (2017). The future distribution of river fish: The complex interplay of climate and land use changes, species dispersal and movement barriers. *Global Change Biology*, 23(11), 4970–4986. https://doi.org/10.1111/gcb.13760

Radinger, J., Holker, F., Horky, P., Slavik, O., & Wolter, C. (2018). Improved river continuity facilitates fishes' ability to track future environmental changes. *Journal of Environmental Management*, 208, 169–179.

Rahel, F., & Hubert, W. (1991). Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: Biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society*, 120, 319–332. https://doi.org/10.1577/1548-8659(1991)120<0319:FAAHGI>2.3.CO;2

Rahel, F., & McLaughlin, R. (2018). Selective fragmentation and the management of fish movement across anthropogenic barriers. *Ecological Applications*, 28(8), 2066–2081. https://doi.org/10.1002/eap.1795

Reiser, D., & Peacock, T. (1995). A technique for assessing upstream fish passage problems at small-scale hydropower developments. In W. Olson, R. G. White, & R. H. Hamre (Eds.), *Symposium on small hydropower and fisheries* (pp. 423–432). Bethesda, MD: American Fisheries Society, Western Division.

Rhoades, C., Entwistle, D., & Butler, D. (2011). The influence of wildfire extent and severity on streamwater chemistry, sediment and temperature following the Hayman Fire, Colorado. *International Journal of Wildland Fire*, 20(3), 430–442. https://doi.org/10.1071/WF09086

Rieman, B., Isaak, D., Adams, S., Horan, D., Nagel, D., Luce, C., & Myers, D. (2007). Anticipated climate warming effects on bull trout habitats and populations across the interior Columbia River basin. *Transactions of the American Fisheries Society*, 136(6), 1552–1565. https://doi.org/10.1577/T07-028.1

Rieman, B., & McIntyre, J. (1995). Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American Fisheries Society*, 124(3), 285–296. https://doi.org/10.1577/1548-8659(1995)124<0285:OOBTIN>2.3.CO;2

Royle, J., & Kery, M. (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology*, 88, 1813–1823. https://doi.org/10.1890/06-0669.1

Rubenson, E., & Olden, J. (2019). An invader in salmonid rearing habitat: Current and future distributions of smallmouth bass (*Micropterus dolomieu*) in the Columbia River Basin. *Canadian Journal of Fisheries and Aquatic Sciences*. https://doi.org/10.1139/cjfas-2018-0357

Sala, O., Chapin, F., Armesto, J., Berlow, E., Bloomfield, J., Dirzo, R., ... Leemans, R. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770–1774.

Schloss, C., Nuñez, T., & Lawler, J. (2012). Dispersal will limit the ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences of the United States of America*, 109(22), 8606–8611.

Schmetterling, D., & Adams, S. (2004). Summer movements within the fish community of a small montane stream. *North American Journal of Fisheries Management*, 24(4), 1163–1172. https://doi.org/10.1577/M03-025.1

Selong, J., McMahon, T., Zale, A., & Barrows, F. (2001). Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Transactions of the American Fisheries Society*, 130(6), 1026–1037. https://doi.org/10.1577/1548-8659(2001)130<1026:EOTOGA>2.0.CO;2

Shepard, B., Sanborn, B., Ulmer, L., & Lee, D. (1997). Status and risk of extinction for westslope cutthroat trout in the upper Missouri River basin, Montana. *North American Journal of Fisheries Management*, 17(4), 1158–1172. https://doi.org/10.1577/1548-8675(1997)017<1158:SAROEF>2.3.CO;2

Stewart, I. (2009). Changes in snowpack and snowmelt runoff for key mountain regions. *Hydrological Processes: An International Journal*, *23*(1), 78–94.

Thomas, C., Cameron, A., Green, R., Bakkenes, M., Beaumont, L., Collingham, Y., ... Hughes, L. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145–148.

Thuiller, W., Lavore, S., Araújo, M., Sykes, M., & Prentice, I. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(23), 8245–8250. https://doi.org/10.1073/pnas.0409902102

Tingley, M., Koo, M., Moritz, C., Rush, A., & Beissinger, S. (2012). The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology*, *18*(11), 3279–3290. https://doi.org/10.1111/j.1365-2486.2012.02784.x

Tittensor, D., Mora, C., Jetz, W., Lotze, H., Ricard, D., Berghe, E., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, *466*(7310), 1098. https://doi.org/10.1038/nature09329

Utzinger, J., Roth, C., & Peter, A. (1998). Effects of environmental parameters on the distribution of bullhead *Cottus gobio* with particular consideration of the effects of obstructions. *Journal of Applied Ecology*, *35*, 882–892. https://doi.org/10.1111/j.1365-2664.1998.tb00006.x

Valtonen, A., Hirka, A., Szőcs, L., Ayres, M., Roininen, H., & Csóka, G. (2017). Long-term species loss and homogenization of moth communities in Central Europe. *Journal of Animal Ecology*, *86*(4), 730–738. https://doi.org/10.1111/1365-2656.12687

WDFW. (2009). *Fish passage barrier and surface water diversion screening assessment and prioritization manual*. Olympia WA: Washington State Department of Fish and Wildlife, 240 pp.

Wenger, S. J., Isaak, D. J., Luce, C. H., Neville, H. M., Fausch, K. D., Dunham, J. B., ... Williams, J. E. (2011). Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(34), 14175–14180. https://doi.org/10.1073/pnas.1103097108

Westerling, A., Hidalgo, H., Cayan, D., & Swetnam, T. (2006). Warming and earlier spring increase western US forest wildfire activity. *Science*, *313*(5789), 940–943.

White, G., & Burnham, K. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, *46*(sup1), S120–S139. https://doi.org/10.1080/00063659909477239

Wilcox, T., Young, M., McKelvey, K., Isaak, D., Horan, D., & Schwartz, M. (2018). Fine-scale environmental DNA sampling reveals climate-mediated interactions between native and invasive trout species. *Ecosphere*, *9*(11), e02500.

Williams, J., Haak, A., Neville, H., & Colyer, W. (2009). Potential consequences of climate change to persistence of cutthroat trout populations. *North American Journal of Fisheries Management*, *29*(3), 533–548. https://doi.org/10.1577/M08-072.1

Wohl, E., Lininger, K., & Baron, J. (2017). Land before water: The relative temporal sequence of human alteration of freshwater ecosystems in the conterminous United States. *Anthropocene*, *18*, 27–46. https://doi.org/10.1016/j.ancene.2017.05.004

Young, M., Isaak, D., McKelvey, K., Wilcox, T., Bingham, D., Pilgrim, K., ... Schwartz, M. (2016). Climate, demography, and zoogeography predict introgression thresholds in salmonid hybrid zones in Rocky Mountain streams. *PLoS One*, *11*, e0163563. https://doi.org/10.1371/journal.pone.0163563

Young, M., McKelvey, K., Pilgrim, K., & Schwartz, M. (2013). DNA barcoding at riverscape scales: Assessing biodiversity among fishes of the genus *C ottus* (*T eleostei*) in northern Rocky Mountain streams. *Molecular Ecology Resources*, *13*(4), 583–595.

Zeller, K., McGarigal, K., & Whiteley, A. (2012). Estimating landscape resistance to movement: A review. *Landscape Ecology*, *27*(6), 777–797. https://doi.org/10.1007/s10980-012-9737-0

Zwick, P. (1992). Stream habitat fragmentation—A threat to biodiversity. *Biodiversity & Conservation*, *1*(2), 80–97. https://doi.org/10.1007/BF00731036

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.