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ARTICLE

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Do metapopulations and management matter for relict headwater bull trout populations in a warming climate?

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Abstract

Mountain headwater streams have emerged as important climate refuges for native cold-water species due to their slow climate velocities and extreme physical conditions that inhibit non-native invasions. Species persisting in refuges often do so as fragmented, relict populations from broader historical distributions that are subject to ongoing habitat reductions and increasing isolation as climate change progresses. Key for conservation planning is determining where remaining populations will persist and how habitat restoration strategies can improve biological resilience to enhance the long-term prospects for species of concern. Studying bull trout, a headwater species in the northwestern USA, we developed habitat occupancy models using a data set of population occurrence in 991 natal habitat patches with a suite of novel geospatial covariates derived from high-resolution hydroclimatic scenarios and other sources representing watershed and instream habitat conditions, patch geometry, disturbance, and biological interactions. The best model correctly predicted bull trout occupancy status in 82.6% of the patches and included effects for: patch size estimated as habitat volume, extent of within-patch reaches <9°C mean August temperature, distance to nearest occupied patch, road density, invasive brook trout prevalence, patch slope, and frequency of high winter flows. The model was used to assess 16 scenarios of bull trout occurrence within the study streams that represented a range of restoration strategies under three climatic conditions (baseline, moderate change, and extreme change). Results suggested that regional improvements in bull trout status were difficult to achieve in realistic restoration strategies due to the pervasive nature of climate change and the limited extent of restoration actions given their high costs. However, occurrence probabilities in a subset of patches were highly responsive to restoration actions, suggesting that targeted investments to improve the resilience of some populations may be contextually beneficial. A possible strategy, therefore, is focusing effort on responsive populations near more robust population strongholds, thereby contributing to local enclaves where dispersal among populations further enhances resilience. Equally important, strongholds constituted a small numerical percentage of patches (5%–21%), yet encompassed the large majority of occupied habitat by volume (72%–89%) and their protection could have significant conservation benefits for bull trout.

KEYWORDS
bull trout, climate change, connectivity, metapopulation, patch occupancy model, refugia

INTRODUCTION

Global biodiversity loss is an ongoing and pervasive process caused by a changing climate, human land uses that degrade or destroy natural habitats, and the introduction and spread of invasive species that displace native species (Urban, 2015; Villéger et al., 2011; Vorosmarty et al., 2010). For freshwater stream taxa that require cold temperatures, this often translates to the truncation of former ranges at downstream extents and persistence in mountain headwater streams as increasingly disjunct relict populations (Fausch, 2008; Quaglietta et al., 2018; Young et al., 2016). Although confinement to headwaters, especially in an era of global warming, has been viewed as antithetical to long-term persistence (Buisson et al., 2008; Domisch et al., 2011; La Sorte & Jetz, 2010), recent research indicates that the slow climate velocities typical of steep mountain streams make them resistant climate refuges for a variety of taxa (Isaak et al., 2016; Muhlfeld et al., 2020; Sharma et al., 2021; Troia et al., 2019). Moreover, such locations appear to be more resistant to nonnative species invasions and less subject to many forms of habitat degradation than are lowland streams because of their climatically extreme conditions and high stream power (Isaak et al., 2015; Margesin & Schinner, 1999; Montgomery & Buffington, 1997). Yet because of the isolation of headwater populations, their juxtaposition relative to other populations and the potential this provides for demographic exchange takes on added significance for understanding and forecasting persistence.

Metapopulation theory provides a framework to interpret spatial population dynamics in light of habitat patch size and connectivity to other patches (i.e., habitat geometry; Hanski, 1991; Hanski & Ovaskainen, 2003). Metapopulations are thought to form when there is variation in demographic rates among geographically discrete subpopulations that are nonetheless linked by dispersal (Schtickzelle & Quinn, 2007). Because aquatic taxa in headwater habitats are often naturally fragmented and occupy dynamic landscapes, metapopulation concepts have frequently been applied to these taxa (Falke & Fausch, 2010; Isaak et al., 2007; Mari et al., 2014; Rieman & Dunham, 2000; Rieman & McIntyre, 1993, 1995; Woodford & McIntosh, 2010). The kind of metapopulation that develops is often evident from patterns of patch occupancy, extinction, and recolonization. For some taxa, variation in patch occupancy is strictly a function of rates of extinction and colonization (i.e., classical metapopulations; Levins, 1969). For others, such as salmonid fishes, mainland-island metapopulation structures may be more fitting because of the correlation between patch size and population persistence (Dunham & Rieman, 1999; Peterson et al., 2014; Rieman & McIntyre, 1995).

A useful application of metapopulation theory for aquatic species has been the implementation of probabilistic statistical models that predict patch occupancy based on habitat geometry and dispersal processes (Dunham, Rieman, et al., 2002; Knapp et al., 2003). These models often include measures of habitat patch quality for which each covariate in the model represents an ecological hypothesis that can be tested and ranked relative to other covariates (Austin, 2002; Hanski & Ovaskainen, 2003). Increasingly powerful models are now possible for lotic environments, especially where study domains encompass large areas, because of marked progress over the last decade in the availability and sophistication of geospatial tools and data sets for describing streams and rivers (Fisher, 2013; McKay et al., 2012). Whereas early models were often limited to covariates originally developed for terrestrial applications, contemporary researchers now have hundreds of stream specific attributes from which to choose (Domisch et al., 2015; González Vilas et al., 2016; Hill et al., 2016). Particularly relevant for studies assessing climate change are high-resolution stream temperature and flow scenarios to represent the hydroclimatic conditions experienced by stream faunas (Irving et al., 2018; Isaak, Wenger, Peterson, et al., 2017; Wenger et al., 2010). Although temperature is usually the focus of these assessments (Comte et al., 2013), hydrologic changes may also be important, especially in snow-dependent regions trending toward earlier runoff, increased flood variability, and decreased summer flows (Hamlet & Lettenmaier, 2007; Luce & Holden, 2009; Stewart, 2009). Paralleling the development of better stream descriptors has been the accumulation of larger and more extensive biological inventories as new monitoring programs are implemented and data from older, disparate sources are centralized into larger databases (e.g., Global Biodiversity Information Facility [https://www.gbif.org/]; Biodiversity Information

Serving Our Nation [https://bison.usgs.gov/]; Wüest et al., 2020). Accelerating this trend in recent years have been environmental DNA surveys, which when used in conjunction with standardized field and laboratory protocols, provide a rigorous means of crowd-sourcing broad sampling campaigns for target organisms (Isaak, Young, et al., 2018; McKelvey et al., 2016; Young, Isaak, Schwartz, et al., 2018).

Here, we draw on many of these elements to develop a patch occupancy model for bull trout (*Salvelinus confluentus)* populations in the northwestern USA and explore hypotheses about factors affecting its current and potential future distributions. The bull trout is a prototypical headwater species because the cold thermal niche of its juvenile life stage restricts spawning and rearing to patchily distributed habitats in montane networks (Dunham, Rieman, et al., 2003; Rieman & McIntyre, 1995). Bull trout is a species of conservation concern due to broad declines observed in the 20th century (Rieman, Lee, & Thurow, 1997; USFWS, 1999) and because environmental trends related to climate change are now driving upstream range contractions (Al-Chokhachy, Schmetterling, et al., 2016; Eby et al., 2014; LeMoine et al., 2020), accurately predicting what constitutes suitable natal habitat and which of those habitats are likely to be occupied is crucial for prioritizing species conservation efforts. Although a simple bull trout model that we developed previously (Isaak et al., 2015) was reasonably accurate and indicated that some populations were likely to persist in refuge streams even following extreme climate change, we sought to improve its performance and realism by using more sophisticated and nuanced measures of habitat features, adding covariates to address elements of metapopulation structure, land use, and disturbance, and availing ourselves of new biological inventories, the bulk of which were derived from broad-scale, crowd-sourced eDNA sampling targeted at potential bull trout natal habitats (Young et al., 2017). This refined model was used in a sensitivity analysis of model parameters and with climate projections to create probabilistic scenarios of regional bull trout occurrence. In particular, we were interested in understanding the degree to which habitat geometry affected population occurrence, whether realistic restoration and management interventions could offset future bull trout declines, and how conservation strategies might be improved by this information.

METHODS

Study area

The study area encompassed 128,220 km^2 of mountainous, topographically complex terrain that spans elevations from 300 to 3700 m across 42° to 49° N latitude in the Rocky Mountains of the northwestern United States (Figure 1; Appendix S1). Climate in the area is characterized by cold, wet winters with moderate to heavy snow accumulations at high elevations and warm, dry summers. Vegetation is dominated by coniferous forests except at low elevations and south-facing aspects where grasses and shrubs are most common. Wildfires burned 13.6% of the study area from 1996 to 2015 and have historically been common within the region but have recently begun advancing into higher elevations spurred by a warming climate (Alizadeh et al., 2021; Westerling, 2016). Most of the study area is publicly owned and federally administered by the United States Forest Service (71%), Bureau of Land Management (12%), Bureau of Indian Affairs (6%), and National Park Service (1%) for a variety of land-use, recreational, and conservation purposes. Human population densities are low except along wider segments of river valleys where fertile floodplains and easy access to water enhance agriculture and ranching. In contrast with a relatively sparse paved highway system, a dense network of unpaved roads was developed in many drainages to facilitate timber harvest activities during the second half of the 20th century (Roper et al., 2018; Swanson, 2015). Not all basins have been harvested, however, as many were too remote or rugged to prove economical, whereas others are formally protected as designated wilderness areas and national parks where anthropogenic activities are restricted (Swanson, 2015). Although stream environments in many areas still bear the marks of various land-use activities, trends in recent decades also suggest a general improvement in the habitat conditions in response to protective measures implemented regionally for several fish species of concern (Roper et al., 2019).

Hundreds of individual streams drain the study area and constitute a perennial network that exceeds 50,000 km in length. The topographic and climatic diversity of the region results in a wide range of stream thermal conditions. For example, although streams exhibit winter temperatures that are consistently near 0°C, mean summer temperatures range from 4.0 to 27.0°C (Isaak, Luce, Chandler, et al., 2018). Stream hydrographs are typical of snowmelt runoff systems, with high flows in the spring and low flows during late summer, fall, and winter. Basins at higher elevations exhibit peak runoff several weeks later than basins of comparable size at lower elevations due to colder air temperatures and persistent snowfields (Hamlet & Lettenmaier, 2007). Fish communities are relatively simple, often consisting of five or fewer species, especially in the colder headwater rivers and streams where spawning and rearing by bull trout occurs. Other trout species that can influence bull trout distributions via

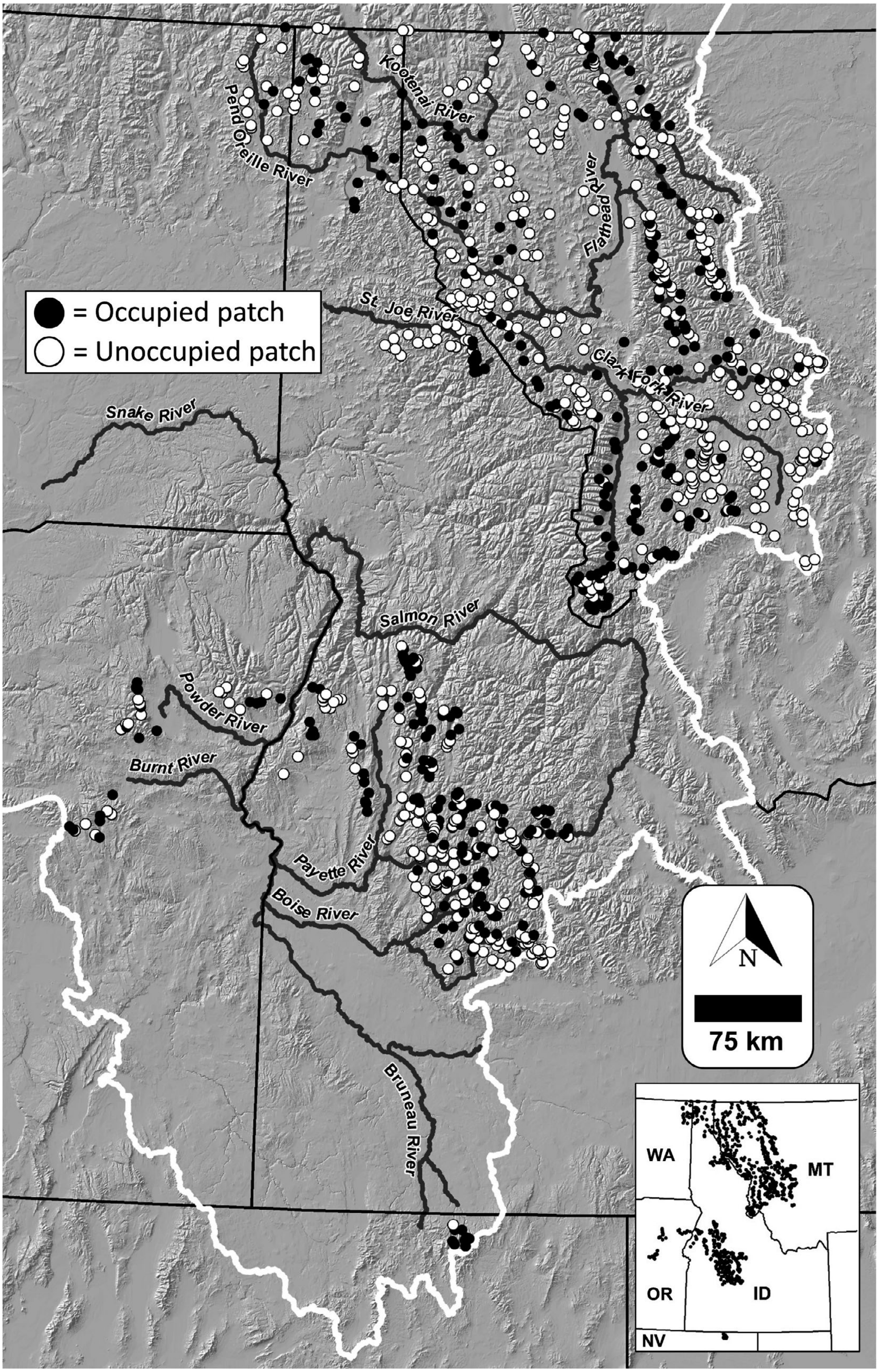

FIGURE 1 Occupancy status of 991 bull trout natal habitat patches in a data set from the Rocky Mountains in the northwestern United States that was used to develop an occupancy model. The study area constitutes the southeastern corner of the bull trout range, which is denoted by the heavy white line. The data set is also available as a high-resolution poster image (Appendix S1)

competition, predation, or hybridization are native and introduced populations of rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*Oncorhynchus clarkii*), as well as the introduced brown trout (*Salmo trutta*) and brook trout (BKT) (*Salvelinus fontinalis*). BKT are especially problematic because of their relatively cold yet broad thermal niche (Durhack et al., 2021; Isaak, Wenger, & Young, 2017) and preference for small streams that are most commonly occupied by bull trout (Rieman et al., 2006; Warnock & Rasmussen, 2013; Wilcox et al., 2018).

Although adult bull trout may move extensively throughout river networks where fluvial connectivity is not impeded by dams or other barriers (Howell et al., 2010; Monnot et al., 2008), they are philopatric and spawning and juvenile rearing occur almost exclusively where mean summer water temperatures rarely exceed 11°C (Isaak, Wenger, & Young, 2017; Rieman et al., 2006) due to the restricted thermal tolerances of embroyos (Dahlke et al., 2020). As a result, individual bull trout populations are often delineated based on discrete natal habitats in which the downstream boundaries are set by a temperature threshold or elevation proxy (Dunham, Rieman, et al., 2002; Isaak et al., 2015; Rieman & McIntyre, 1995). In these areas, adults excavate nests within the stream substrates and deposit eggs during the late summer and early fall, the eggs incubate during the winter, and young fish emerge the following spring. At this point, juvenile individuals adopt one of two life histories (Downs et al., 2006; Rieman & McIntyre, 1993), although many populations are thought to support both life history forms (Howell et al., 2016; Nelson et al., 2002). Migratory individuals rear in their natal streams for two or more years, then move downstream to more productive habitats where growth is rapid and eventually return to spawn as relatively large adults (>400 mm total length). Resident individuals remain in natal streams and mature as much smaller adults (<200 mm).

Bull trout natal patches

High data densities were required to adequately assess bull trout patch occupancy and connectivity among populations, so we confined our analysis to three areas with comprehensive surveys of nearly all natal habitats: the middle Snake River of northern Nevada, southwestern Idaho, and southeastern Oregon; the western portions of the Salmon River basin in central Idaho; and the United States portion of the Columbia River headwaters in northern Idaho and northwestern Montana (Figure 1). Other river basins between these areas also support bull trout populations, but were dominated by remote wilderness areas in central Idaho where fish survey data are less prevalent. ArcGIS shapefiles depicting an initial set of bull trout natal habitat patches within the study basins were downloaded from the Climate Shield website for a baseline historical climate period representing the late 20th century (https://www.fs.fed.us/rm/boise/AWAE/projects/ClimateShield.html). These habitat patches were developed previously by Isaak et al. (2015) from the 1:100,000-scale National Hydrography Data set-Plus (NHD-Plus; https://nhdplus.com/NHDPlus/) and consisted of spatially contiguous stream reaches >3 km that met three criteria: (1) mean August stream temperatures <11°C; (2) summer discharge rates >0.0057 m^3/s (roughly equivalent to a low-flow wetted width of 1 m based on empirical relationships in Peterson et al., 2013) to represent habitats large enough to be occupied by fish; and (3) reach slopes <15% to ensure areas were likely to have suitable spawning habitats and were not too steep for ascent and occupation by trout species. These patch criteria were based on our observations during field research and patterns of fish species occurrence at thousands of stream survey sites that have previously been linked to the NHD-Plus network (Isaak et al., 2015; Isaak, Wenger, & Young, 2017; Wenger et al., 2011). Application of the criteria also negated the potential utility of higher-resolution network data sets such as the 1:24,000-scale NHD that that depict many additional headwater reaches upstream from the terminus of fish distributions.

Because the size of habitat patches is often the strongest predictor of bull trout occurrence (Dunham & Rieman, 1999; Isaak et al., 2015), the initial patch set was edited to remove reaches within patches that were upstream of geological barriers that blocked historical fish access such as vertical waterfalls or continuous sections of high velocity cascades and near-vertical drops. Waterfall locations were obtained from the World Waterfall database (https://www.worldwaterfalldatabase.com/), interviews with local fisheries biologists, and our knowledge of the study streams. Steep cascade sections were identified along the NHD-Plus streamlines using a high-resolution stream slope data set developed for the western USA with a custom script and the 30-m National Elevation Data set (http://ned.usgs.gov/; Appendix S2). We also excluded intermittent reaches where stream channels are usually dry during summer months (Hafen et al., 2020) and identified these based on our personal experience, interviews with local biologists, and a flow-coding field in the NHD-Plus (Fcode = 46003 denotes intermittent reaches). This editing process resulted in a revised set of 1224 potential bull trout natal habitat patches within the study area.

Bull trout have been intensively studied and inventoried since being listed in 1999 as threatened under the

Endangered Species Act (USFWS, 1999). Many of those data sets collected in the 1990s and 2000s, including summer electrofishing surveys of 4521 reaches, were published previously and repurposed for this study to assign bull trout occupancy status to 505 natal patches (Buchanan et al., 1997; Howell et al., 2018; Isaak et al., 2015). These data were supplemented with analyses of 5336 eDNA samples collected during summers from 2015 to 2019 in 399 patches as part of the Rangewide Bull Trout eDNA Project (Young et al., 2017; https://www.fs.fed.us/rm/boise/AWAE/projects/BullTrout_eDNA.html). In patches sampled by electrofishing, the potential for assigning absences incorrectly (i.e., bull trout were in a patch but not detected) was controlled at a rate ≤0.1 by requiring that each patch have a minimum number of sample sites (two to six sites, depending on patch size, although the average number of sites was nine; Isaak et al., 2015). False absence rates from the eDNA surveys were lower because detection rates are higher (e.g., the probability of detecting bull trout at a density of one fish/100 m of stream is 0.85; Wilcox et al., 2016), a recently developed assay affords even greater sensitivity (Dysthe et al., 2018), and we sampled at 1-km intervals throughout patches to maximize detections (McKelvey et al., 2016). We inferred occupancy of a natal habitat patch by juveniles or reproductive adults if we observed eDNA-based detections at three consecutive sites (consistent with our minimum patch size designation) because patches occupied by transient bull trout tend to result in sporadic detections (McKelvey et al., 2016).

Where patch occupancy by bull trout could not be determined because eDNA and electrofishing samples were lacking, detailed maps of patches and river basin stream networks were developed to highlight the areas of uncertainty and used as the basis for interviews with biologists that had first-hand knowledge of the streams in question. In a small number of streams ($n = 27$), bull trout populations extended downstream of predefined 11°C patch boundaries, so these were extended to fully encompass the populations. In 17 additional instances, occupied natal habitats, often immediately adjacent to lakes or mainstem rivers, were smaller than the 3-km minimum patch size in the Isaak et al. (2015) data set and patches were created to encompass these populations. The final data set consisted of 991 patches for which the occupancy status of bull trout was known (Figure 1; Appendix S1). Because BKT may affect bull trout distributions (Rieman et al., 2006; Wilcox et al., 2018), we also recorded information about their spatial prevalence within patches from available data sources. Prevalence was calculated as the percentage of sites where BKT occurred when four or more surveys were available within a patch. For patches with fewer surveys, biologists were asked to describe the prevalence of BKT as absent from a patch, at low abundance (present at 1%–50% of sites within a patch), or at high abundance (present at >50% of sites within a patch) and these were assigned percentages of 0%, 25%, or 75%, respectively, to enable merging with information from patches where surveys were more common.

Attributes of the natal habitat patches were described primarily from previously published, publicly available geospatial data sets that were compatible with the 1:100,000-scale NHD-Plus network. For an attribute to be considered, we required that there be a plausible hypothesis of its effect on bull trout occurrence based either on information in the literature or our observations and understanding of bull trout ecology and distributions (Appendix S3). Attributes included measures of habitat geometry associated with patch size and connectivity, physical habitat characteristics such as average patch slope and elevation, hydrologic characteristics related to runoff timing and variability, thermal conditions, descriptions of internal patch refugia, valley morphology, riparian vegetation composition, wildfire disturbance, and road density. Early patch size estimates for stream fish populations often relied on watershed area as a proxy for stream size (e.g., Dunham, Rieman, et al., 2002) or linear measures of habitat extent (e.g., Hilderbrand & Kershner, 2000) but the recent availability of stream flow scenarios that include discharge estimates (Irving et al., 2018; Wenger et al., 2010) enabled size calculations based on volume. Volume may more consistently portray the amounts of available habitat across geographically broad and climatically diverse areas where water yields vary per unit of watershed area (Bieger et al., 2015; Hortness, 2006) or where geological barriers such as waterfalls restrict populations to downstream portions of otherwise extensive patches (e.g., Hudson et al., 2019). Volumetric estimates may also better describe the biological impacts of climate change where hydrologic characteristics are sensitive to temperature increases as is often the case in mountain headwaters (Stewart, 2009).

Most patch attributes could be summarized from data sets that linked directly to reach segments composing the patches. However, for watershed characteristics such as wildfire prevalence and road density, patch pourpoints were calculated and upstream watersheds delineated to serve as the basis for subsequent summaries. Roads can have negative effects on bull trout that may be evident at different spatial scales (Al-Chokhachy, Black, et al., 2016; Trombulak & Frissell, 2000), so we calculated five road density metric variants at the watershed scale, 100-m patch-buffer scale, road-patch intersection scale, and reach contributing area scale (Appendix S4). Reach contributing areas are similar to watershed contributing areas but pertain only to the smaller portions of watersheds that are directly linked to stream reaches

(McGlynn & Seibert, 2003). For the wildfire prevalence attribute, variants were calculated at the watershed scale and 100-m patch-buffer scale but these were also combined with information about wildfire severity (low, medium, or high) and temporal period (burned during the 10-year period from 2008 to 2017 or burned during the 20-year period from 1998 to 2017) to develop 20 different fire metrics (Appendix S4).

Connectivity, or the accessibility of a patch to organisms from other occupied patches, is fundamental to assessing metapopulation dynamics (Hanski, 1991). Connectivity was represented in an early bull trout occupancy model using a nearest neighbor approach (i.e., the stream distance from a focal patch to the nearest occupied patch; Dunham & Rieman, 1999) but dozens of additional connectivity metrics have been proposed (please refer to reviews by Moilanen & Nieminen, 2002; Prugh, 2009) and have yet to be assessed for relevance to headwater trout populations. These metrics range from the simplest nearest neighbor approaches to complex measures that incorporate estimates of dispersal rates and distances using size-weighting schemes among networks of occupied patches. Drawing on those concepts, we developed 16 connectivity metric variants that were calculable from our data set using information about patch size and stream distances among patch pourpoints (Appendix S4). In instances where dams prevented bull trout movements between patches, interpatch distances were modified accordingly. Locations of dams were obtained from the United States Army Corp of Engineers National Inventory of Dams database (USACOE, 2016; http://nid.usace.army.mil/).

Patch occupancy model

Logistic regression was used to model the probability of bull trout habitat occupancy as a function of patch attributes using Proc Logistic in SAS Version 9.4 (full data set available in Appendix S1). Prior to the main analysis, however, preliminary analyses were conducted to determine the best variant representations of the five road density metrics, 20 wildfire prevalence metrics, and 16 connectivity metrics (Appendix S4). The two metric variants for each of the three attributes that performed best were used in final model development with the broad set of attributes. Logistic regressions were then fitted to different candidate models with covariate subsets and ranked based on Akaike's information criterion (AIC; Akaike, 1974). If a subset of top models was ranked closely by <2 AIC points, the presence of uninformative parameters (probability values >0.15) was considered in the selection of the final model (Arnold, 2010). The area under the curve of the receiver operator characteristic (ROC) was calculated to describe model performance and the ability to discriminate among habitats of varying quality (ROC; Pearce & Ferrier, 2000). When fitting models for comparison, covariates that were strongly correlated (i.e., $r > 0.65$; Appendix S5) were not included in the same model to minimize multicollinearity issues (Dormann et al., 2013) but variance inflation factors were also calculated to assess possible effects on parameter estimates. Although many interactions among covariates were possible, we considered only two that had strong ecological rationales. The first was between patch size and BKT prevalence because invasions are most problematic in the small streams where BKT may become abundant and monopolize resources (Isaak et al., 2015; Warnock & Rasmussen, 2013; Wilcox et al., 2018). The second interaction was between patch size and connectivity because mainland-island metapopulation structure assumes that populations in larger patches are less dependent on connectivity to adjacent populations for population persistence (Schtickzelle & Quinn, 2007).

Because of the geographic breadth of the data set, environmental gradients unrelated to the stream attributes that we considered could also be important, so the spatial coordinates of patch pourpoints (i.e., northing and easting coordinates from the Universal Transverse Mercator system) were added to the pool of covariates. Another spatial effect may relate to the river basin in which a cluster of natal patches occurred if there were locally important conditions associated with underlying geology, past glaciation, lake prevalence, land-use severity, or other factors not represented explicitly by covariates. These basins were treated as a class variable in the logistic regression models and represented as the areas encompassed by the eight-digit hydrologic unit codes (HUC8) in the National Watershed Boundary Data set (Seaber et al., 1987; USGS, 2013). Once a final model had been selected, its predictive accuracy and robustness were assessed by calculating raw classification success and the 10-fold cross-validation classification rate (Stoltzfus, 2011). Relative effect sizes of the covariates in the final model were interpreted based on parameter estimates standardized by their z-scores.

Bull trout scenarios

The final patch occupancy model was used to create 16 scenarios of bull trout occurrence probabilities associated with three climate conditions (Appendix S6). The first set of eight scenarios (S1–S8) assumed baseline climate conditions, and the first of these used the observed covariate values to represent contemporary habitat conditions and bull trout occupancy probabilities. The next six scenarios provided a sensitivity analysis by setting covariate values of model parameters most directly affected by management actions to their observed extremes. Scenario 8 represented a comprehensive restoration strategy in which connectivity among patches was fully restored, road densities were set to zero, and BKT populations were eliminated. Such a scenario is unrealistic because of the high costs and controversy it would entail, but it was useful for insight into the potential status of bull trout in relatively pristine habitat and the number of local population extirpations that may have already occurred. For each scenario, the occupancy model was also used to predict the number of patches that would be occupied by bull trout based on a classification threshold that balanced errors of omission and commission.

A second set of four scenarios (S9–S12) was developed based on moderate climate change conditions in which mean August stream temperatures were increased by 1°C, summer stream discharge decreased by 25%, and the average number of days with winter high flows increased from 3 to 6 days (Appendix S6). Because bull trout natal patch boundaries were delimited by an 11°C threshold, the temperature increase forced these boundaries upstream and fragmented some patches, necessitating recalculation of the number, length, and volume of patches (Appendix S7). Covariate values not associated with hydroclimatic attributes remained at their observed values within the new patch extents for the first of the four scenarios (S9). In the next scenario (S10), an ambitious restoration strategy was represented in which connectivity among patches was fully restored, road densities within all patch watersheds were reduced by 10%, and BKT populations were eradicated from 25% of randomly selected patches that were heavily invaded (>50% BKT prevalence) and relatively small (<10 km stream length). The road reduction target was based on reports from two National Forests in the study area that enacted aggressive road removal programs (Flathead National Forest, 2014; Idaho Panhandle National Forest, 2015), but which were limited from greater reductions by the expense (US $6000–US$8000 per road km) and public opposition to road removals. BKT removal efforts are also expensive (US$8000–US$10,000 per stream km), so these projects are usually targeted at small streams where success rates are highest (Buktenica et al., 2013; Meyer et al., 2006). Scenario 11 was developed to represent another partial restoration scenario but included a higher 25% road removal target that was focused on the same patches selected for BKT removal in Scenario 10. Last, we also simulated a full restoration strategy (S12) such as that used in S8.

A third set of four scenarios (S13–S16) was identical to the second set except that extreme climate change conditions were represented by changing the baseline conditions to reflect a 2°C increase in mean August stream temperatures, a 50% decrease in summer flows, and an increase in the average number of days with winter high flows to 9 days. The moderate and extreme climate change conditions were representative of future conditions that are likely to occur in the latter half of the 21st century or the 22nd century based on trends observed within the study region during the last several decades (Hamlet & Lettenmaier, 2007; Isaak, Luce, Horan, et al., 2018; Leppi et al., 2012; Luce & Holden, 2009) and future projections (Hamlet et al., 2013; Isaak, Wenger, Peterson, et al., 2017). We did not consider more extreme climatic shifts because so little bull trout habitat would remain that conservation and prioritization schemes would be irrelevant.

RESULTS

Of the 991 putative natal bull trout patches in the data set, 390 were occupied, 601 were unoccupied, and patterns of occupancy were well mixed across the study domain (Figure 1). Patch attributes suggested diverse conditions among the habitats (Table 1) and varying degrees of correlation among the attributes and with bull trout occurrence (Appendices S5 and S8). The preliminary analysis indicated that each of the five road density metrics had a statistically significant effect on bull trout occurrence but that RD1 (road length within a patch watershed divided by watershed area) and RD2 (road length within the reach contributing areas adjacent to a patch divided by the area of the reach contributing areas) performed best (Appendix S4). Only six of the 20 wildfire prevalence metrics were statistically related to patch occupancy and distinctions among these six metrics were not substantial. However, WP9 (percentage of a 100-m patch buffer that burned at high severity from 1998 to 2017) and WP19 (percentage of the patch watershed upstream of a pourpoint that burned at high severity from 1998 to 2017) performed slightly better than the other metrics. Half of the connectivity metrics were significant, with C1 (stream distance to the nearest occupied patch) and C6 (number of occupied patches within 50 km) performing best. Notably, those two metrics were among the simplest, and outperformed by a large margin those measures that presumably exhibited greater biological realism (e.g., C11–C16; Appendix S4). These three pairs of metrics were retained for selecting the final occupancy model.

TABLE 1 Descriptive statistics for covariates associated with the 991 bull trout natal patch habitats that were used to develop the occupancy model

Variable	Mean	Median	SD	Minimum	Maximum
Elevation (Ele, m)	1438	1463	358	556	2257
Patch length (PL; km)	15.9	9.50	18.9	0.748	168
Patch volume (PV; m^3)	6658	975	20,511	20	259,163
Minimum temperature (MinT; °C)	8.24	8.26	1.45	4.19	17.8
Valley bottom confinement (VBC; %)	12.3	7.18	15.1	0	97.0
Slope (S; %)	7.28	7.31	2.51	0.619	15.0
Kilometers <5% slope (km <5%; km)	7.51	3.79	10.5	0	93.7
Kilometers <9°C temperature (km <9°C; km)	7.05	3.00	12.3	0	129
Volume <5% slope (Vol. <5%; m^3)	5383	422	19,038	0	252,789
Volume <9°C (Vol. <9°C; m^3)	1683	142	7677	0	146,721
Winter high flow frequency (WHFF; days)	3.45	2.94	2.66	0	12.3
Average flow mass date (AFMD; days after 1 October)	198	196	14.0	164	246
Baseflow index (BI; %)	71.4	71.7	3.57	59.7	80.0
Road density 1 (RD1; km/km^2)[a]	1.16	0.952	1.07	0	5.62
Road density 2 (RD2; km/km^2)[a]	1.22	1.04	1.08	0	5.27
Riparian canopy trees (RCT; %)	44.3	47.1	18.8	0.368	82.7
Wildfire prevalence 9 (WP9; %)[a]	4.17	0	9.69	0	66.9
Wildfire prevalence 19 (WP19; %)[a]	5.74	0	11.0	0	68.7
Connectivity 1 (C1; km to nearest occupied patch)[a]	20.2	13.4	17.0	0.0591	50
Connectivity 6 (C6; occupied patches within 50 km)[a]	5.49	5	4.63	0	25
Brook trout (BKT; %)	34.1	20.5	37.5	0	100
Adfluvial bull trout (Adfluv; 0 or 1)	...	...	...	0	1

Note: Abbreviations and measurement units are in parentheses.

[a]Different variants of the covariate were considered in a preliminary analysis described in Appendix S4. The two variants with the best predictive performance were selected for use in the main analysis and model selection results reported in the text. Road density 1 = road length per unit of watershed area; Road density 2 = road length per unit of reach contributing areas (i.e., subwatersheds that contribute directly to individual reaches); Wildfire prevalence 9 = percentage of 100-m stream buffers within a bull trout patch that experienced high-severity burns from 1998 to 2017; Wildfire prevalence 19 = percentage of a bull trout patch watershed that experienced high-severity burns from 1998 to 2017.

Final model selection

To complete model selection, we fitted 59 candidate models starting with single covariate models and progressing to those of greater complexity (Appendix S9). Many of the top models in the candidate set had ROC values >0.85, which indicated good discriminatory ability. A subset of nine models highlighted several important patterns within the candidate set (Table 2). The top-ranked models included covariates representing both patch geometry and habitat quality, as well as spatial effects associated with local basins and the easting coordinate. Dropping any of these components significantly degraded model performance, although models with habitat geometry and quality covariates (e.g., models 23, 28, and 31) performed markedly better than a pure spatial model (>114 AIC points; model 49). Also noteworthy was that model performance increased when patch size was represented volumetrically rather than linearly (e.g., model 27 versus 31 or model 35 versus 38). The top models in the candidate set provided large improvements (>153 AIC points) over versions of our earlier bull trout patch occupancy model (models 24 and 36; Appendix S10). Eight models within the candidate set ranked within 5.3 AIC points of the top model (Appendix S9) but each of these included at least one uninformative covariate parameter with a probability >0.15. Among these were models that included one of the interaction terms (model 2 with an interaction between patch size and connectivity, model 6 with an interaction between patch size and BKT prevalence), with neither term being statistically significant.

The top-ranked bull trout patch occupancy model included: (1) habitat geometry represented by patch

TABLE 2 Model rankings for a subset of logistic regression models from the full candidate set (Appendix S9) that predict the probability of bull trout occupancy within 991 natal habitat patches

Model	Covariates	ΔAIC	ROC	Comment
1	HUC8, E, PV, km9C, BKT, WHFF, C1, RD1, S	0.0	0.891	Model includes patch geometry, habitat quality, and spatial effects
12	PV, km9C, BKT, AFMD, C1, RD1, BI, S	73	0.850	Model includes patch geometry and habitat quality effects
23	HUC8, E, PV, C1	119	0.855	Model includes patch geometry and spatial effects
24	HUC8, E, PL, MinT, S, BKT, PL × BKT	153	0.837	Model includes spatial effects with patch covariates matching those in Isaak et al. (2015)
27	PV, C1	167	0.812	Model includes patch geometry effects with patch size represented by volume
28	km9C, BKT, WHFF, RD1, S	176	0.800	Model includes habitat quality effects
31	PL, C1	197	0.791	Model includes patch geometry effects with patch size represented by length
36	PL, MinT, S, BKT, PL × BKT	268	0.748	Model includes patch covariates matching those in Isaak et al. (2015)
47	HUC8, E, N, Ele	382	0.714	Model includes covariates representing spatial effects

Note: Models were ranked from most plausible (ΔAIC = 0) to least plausible, and the receiver operator characteristic (ROC) provides a measure of model performance across a range of sensitivities and specificities. Model 1 was selected to create scenarios assessing climate change and management restoration actions.

TABLE 3 Parameter estimates (*b*) and classification accuracy of the final logistic regression model predicting bull trout occupancy in 991 natal habitat patches

Covariate[a]	*b*	SE	*p*-value	Standardized *b*	Accuracy[b]
Intercept	17.9	6.44	0.01	...	82.6% (79.0%)
PV	8.2×10^{-5}	2.0×10^{-5}	<0.01	0.921	...
km9C	0.101	0.0163	<0.01	0.686	...
E	-1.14×10^{-5}	4.58×10^{-6}	0.01	−0.631	...
C1	−0.0385	0.00695	<0.01	−0.361	...
RD1	−0.596	0.111	<0.01	−0.352	...
BKT	−0.0148	0.00299	<0.01	−0.305	...
S	−0.164	0.0420	<0.01	−0.227	...
WHFF	−0.122	0.0468	0.01	−0.179	...

Note: Covariates are ordered from top to bottom based on the absolute values of the standardized parameter estimates.
[a]Model also includes a categorical effect for the 30 eight-digit hydrologic unit watersheds in which a patch occurred. Hydrologic unit watershed codes were from Seaber et al. (1987).
[b]Classification accuracy at a threshold of 0.43 that balanced errors of omission and commission based on the full data set and 10-fold cross-validation (in parentheses).

volume and the C1 connectivity metric, (2) habitat quality represented by the length of a patch <9°C, road density, BKT prevalence, patch slope, and winter high flow frequency, and (3) spatial effects represented by easting and HUC8 (Table 3). The signs of the parameter estimates were consistent with hypothesized effects (Appendix S3) and VIF values were <2, suggesting that multicollinearity did not adversely affect the parameter estimates. The three most important covariates based on the absolute values of the standardized parameters were patch volume, length of a patch <9°C, and easting coordinate. Connectivity, road density, and BKT prevalence had moderate effects, whereas effects due to patch slope and winter high flow frequency were the smallest. Absent from the best-fitting models were covariates representing fire prevalence, presence of adfluvial life histories, extent of unconfined valley bottoms, elevation, and riparian canopy. The model correctly predicted occupancy status of bull trout in 82.6% of the patches at a classification threshold of 0.43, which balanced errors of omission and commission. Ten-fold cross-validation suggested that the model was robust, with classification accuracy only dropping to 79% when predictions were made on independent data subsets. Response curves show the relationships predicted by model covariates across the ranges of patch attribute values observed in the data set (Figure 2).

Scenario results

For baseline climate and current habitat conditions (S1), the model predicted mean and median bull trout occupancy probabilities in the 991 patches of 0.38 and 0.28, respectively (Figure 3a). The model also predicted that 380 of these patches would be occupied based on the 0.43 probability threshold and that 209 of these patches had high probabilities of occurrence (>0.75). Scenarios simulating the removal of all roads (S2) or BKT populations (S4) measurably increased overall probabilities and the number of patches predicted to be occupied. In the full restoration scenario (S8), mean and median probabilities both improved to 0.56 and the number of occupied patches increased by 75% to 605 from the S1 scenario. Conversely, scenarios representing further degradation of patch quality from current conditions by extensive road building (S3), BKT invasions (S5), or disconnection of patches (S7) indicated the potential for substantial declines based on decreases in occupancy probabilities and the number of occupied patches.

Under moderate climate change conditions and assuming no restoration, occurrence probabilities were predicted to decrease from baseline conditions (S9 probability mean = 0.27 and median = 0.15; Figure 3b) and exhibited minimal improvement (<0.02 increase in probabilities) under the two partial restoration scenarios (S10 and S11). Counterintuitively, the number of occupied patches was predicted to remain similar to the baseline S1 scenario, but this occurred with a reduced overall occupancy rate because fragmentation increased the number of available patches from 991 to 1434. In this context, maintaining bull trout probabilities at levels comparable with current conditions and even increasing the number of occupied patches were possible but required the full suite of restoration actions (S12). Under the extreme climate change conditions (S13–S16; Figure 3c) all indicators of

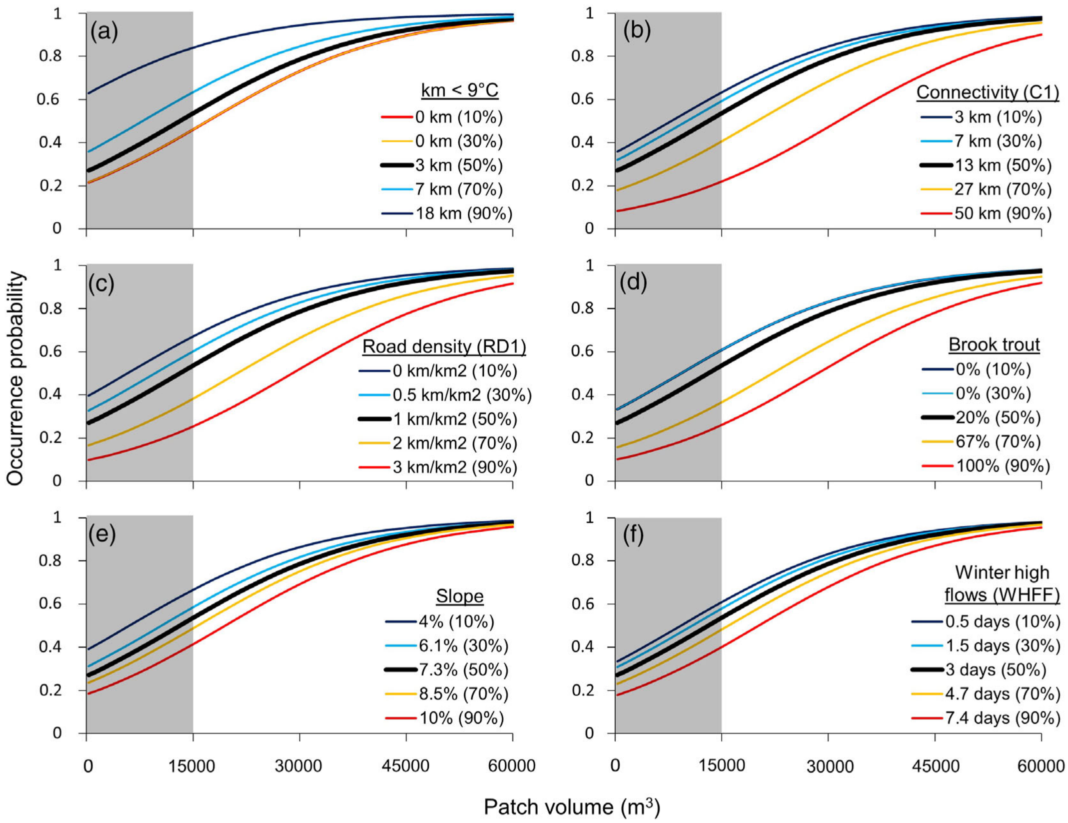

FIGURE 2 (a-f) Response curves from the logistic regression model predicting bull trout occupancy in natal habitat patches. Each curve in a set is based on a percentile in the observed range of covariate values and relationships are conditioned on median values of the other covariates in the model. Gray boxes span the lower 90% of the patch volume range in the data set

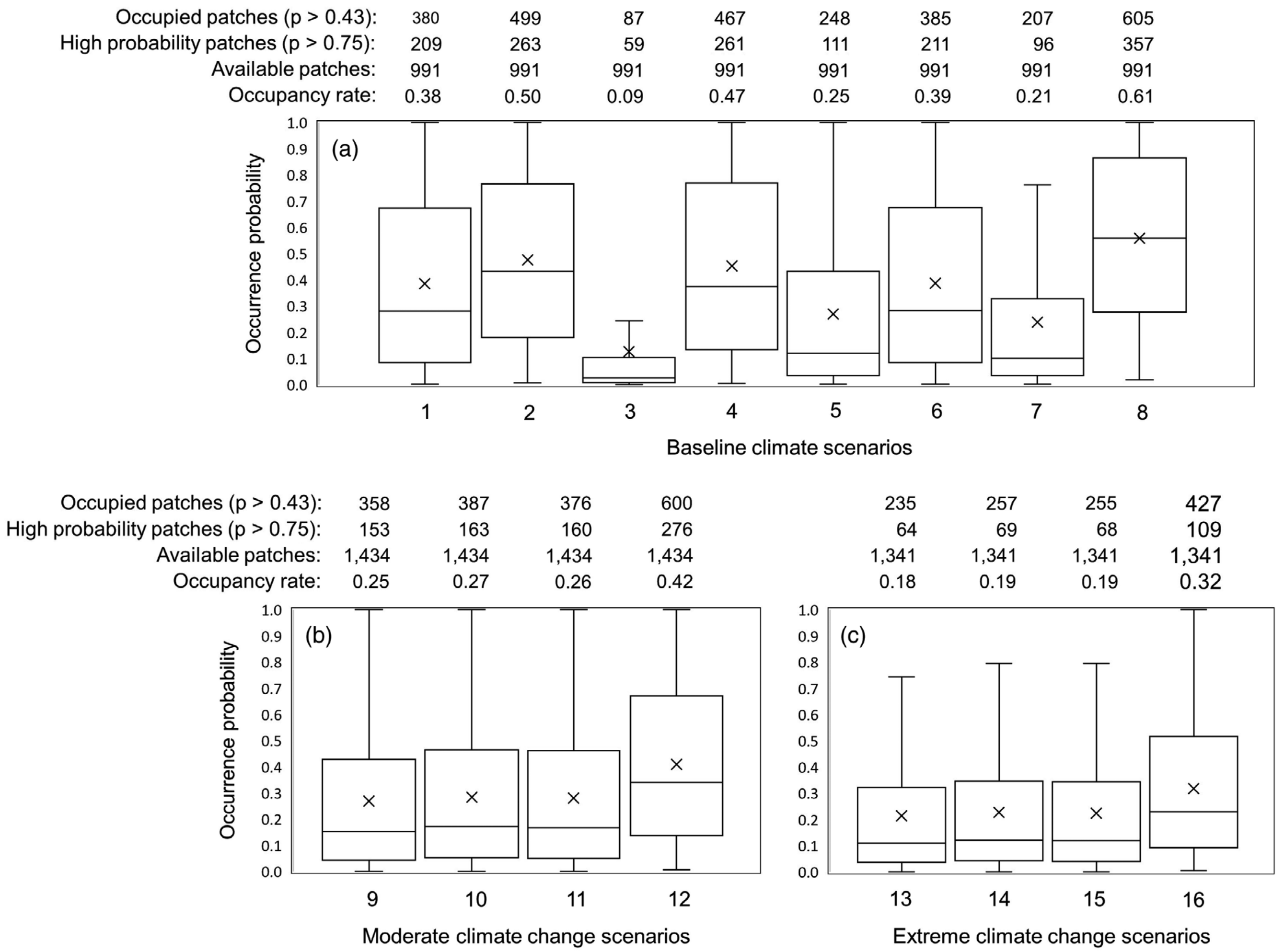

FIGURE 3 (a, b) Summary of predicted bull trout patch occupancy rates and probabilities for 16 habitat restoration and climate change scenarios. Average probability values in the box-and-whisker plots are denoted by 'x' and median values are lines bisecting the boxes. Box boundaries represent the central 50% of observations, and whiskers denote the extremes. Note that the number of available patches increases in the moderate and extreme climate conditions as warming causes fragmentation. Scenario descriptions are provided in Appendix S6

bull trout populations showed declines regardless of restoration efforts, although 64–109 patches retained high probabilities of occupancy >0.75.

Underlying the scenario results were hydroclimatic changes that provide important context. Despite higher numbers of available patches in the climate change scenarios, the total amount of habitat within patches decreased systematically (Figure 4). Declines based on patch volume, however, were exponential compared with the linear declines exhibited by patch length, a discrepancy that occurred because the larger downstream portions of patches were the first to be rendered unsuitable by temperature increases. Also noteworthy were the larger proportions of available habitat that were predicted to be occupied in the volumetric summaries (58%–87%) compared with linear summaries (35%–63%), which highlighted the preference of bull trout for larger volume habitats and the disproportionate importance such habitats are likely to have within the species range. To that point, 89% of the occupied habitat volume in baseline climate scenario S1 was encompassed by 21% of the patches on a numerical basis that had occurrence probabilities >0.75 (Figure 4a). This disproportionate effect remained in the climate change scenarios where 72%–79% of the habitat predicted to be occupied was contained in 5%–11% of the patches.

Another key aspect of the scenarios was the large variation among patches in bull trout probability responses to habitat restoration, which was described by plotting the probability differences between S1 (baseline climate and habitat conditions) and S8 (baseline climate and full restoration) relative to the S1 probabilities (Figure 5). The resulting wedge-shaped pattern was caused by the limitation that high initial probabilities set on subsequent probability increases, and the greater scope for improvements that was possible in many lower probability patches where some level of habitat degradation had occurred. Notably, a

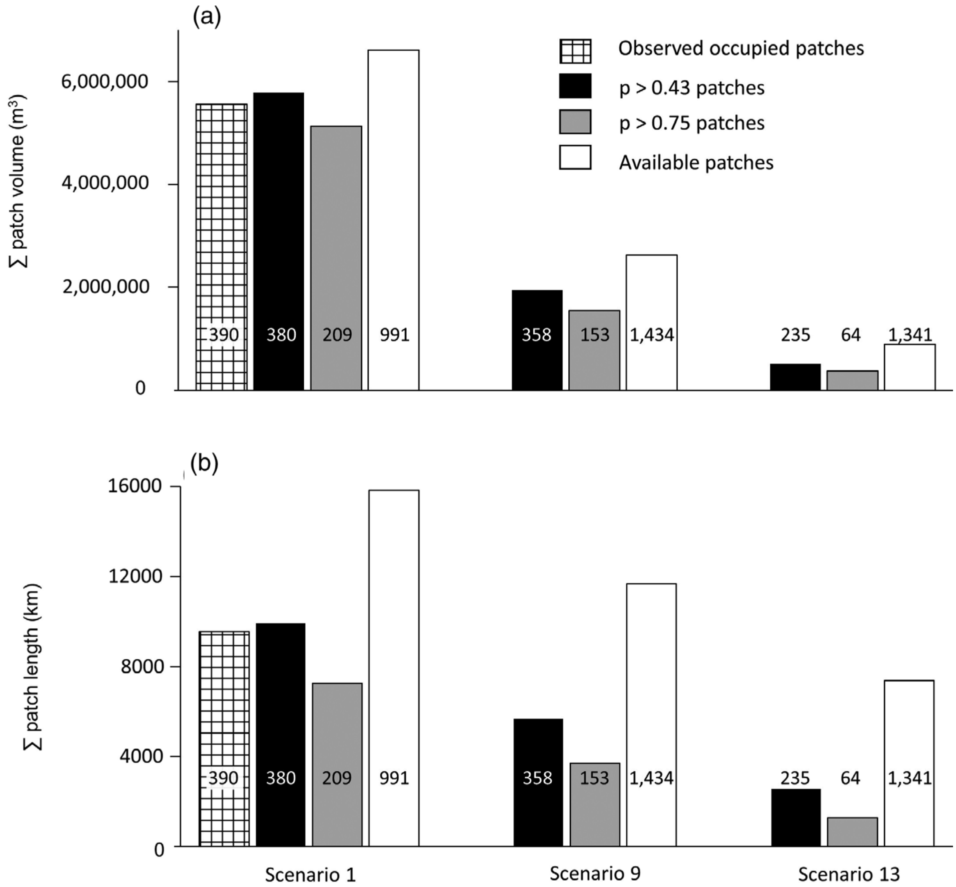

FIGURE 4 Change in total volume (a) and length (b) of available and occupied bull trout patches for current conditions (S1), moderate change (S9), and extreme change (S13) scenarios without restoration actions. Labels on bars indicate the number of patches in each summary

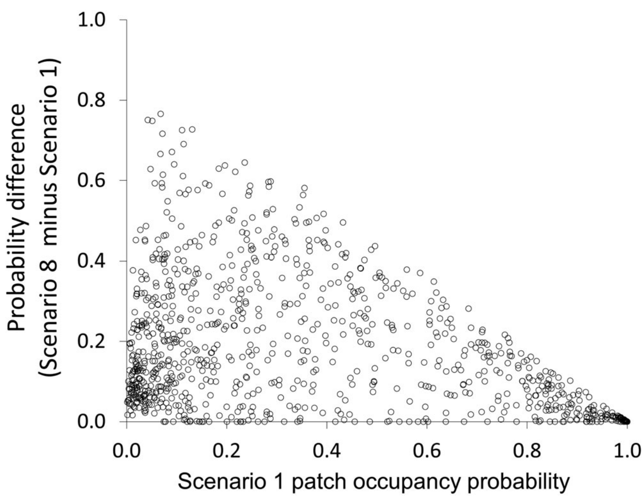

FIGURE 5 Changes in patch-scale bull trout occurrence probabilities between fully restored habitats (Scenario 8) and current habitats (Scenario 1) under baseline climate conditions

dense cluster of patches near the axes origins exhibited limited restoration responses; such patches were typically small, steep, and unlikely to be occupied even if habitat conditions were pristine, therefore would seem to be poor choices for restoration work. When mapped, geographic disparities in response potential across the study domain became evident, both within and among river basins (Figure 6). Complimenting that information are the locations of patches with high probabilities of future occupancy that may serve as long-term climate refuges and sources of dispersal to adjacent populations given the importance of connectivity. However, these patches were relatively rare, irregularly distributed across the study area, and often disjunct from patches with the greatest restoration potential (Figure 6b,c; Appendix S11).

DISCUSSION

Habitats that remain cold throughout the year are critical for life cycle completion and population persistence of many headwater species globally (Meyer et al., 2007; Richardson, 2019). For bull trout, their cold natal patch habitats comprised ~31% of the perennial network length but will continue to shrink as climate change progresses,

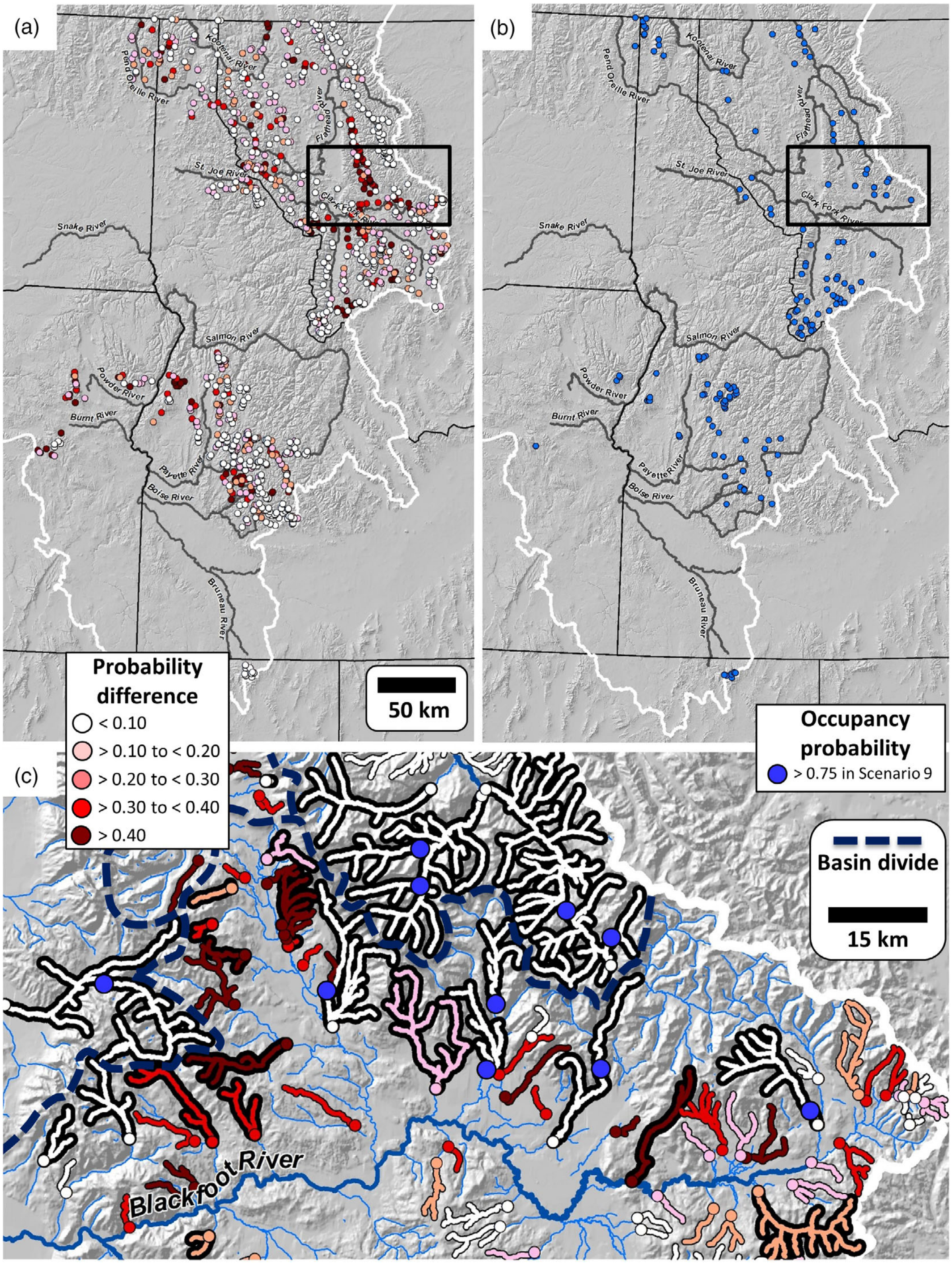

FIGURE 6 Bull trout occupancy probability increases for 991 patches from habitat restoration (Scenario 8 minus Scenario 1, panel (a)) and locations of 153 patches with high occupancy probabilities under moderate climate conditions in Scenario 9 (panel (b)). Details of the inset box are shown in panel (c), which also highlights the locations of extant populations (patches with thick black borders; dots denote the downstream pourpoints of moderate climate condition patches) and basin divides that affect interpatch distances. High-resolution images of bull trout patch occupancy probabilities for all scenarios are provided in Appendix S11

so determining where populations may persist and the most effective habitat restoration policies are fundamental to conservation efforts. Our findings here and in earlier research (Isaak et al., 2015; Young, Isaak, Spaulding, et al., 2018) are encouraging in that, even with a lack of restoration efforts in some scenarios, a subset of patches are predicted to maintain high probabilities of future occupancy and can serve as climate refuges, at least under the suite of conditions that are at this time considered realistic for moderate to extreme climate change (Hamlet et al., 2013; Isaak, Wenger, Peterson, et al., 2017; Wuebbles et al., 2017). Moreover, restoration actions such as those typically deployed in headwater areas can increase the likelihood that some patches will support populations but their judicious application will be required for effect within budgetary, social, and management agency constraints. For example, although a complete restoration scenario under moderate climate change suggested that the current regional status of bull trout could largely be maintained, investments to achieve this are not realistic given attendant costs. Even the less aggressive partial restoration scenarios we considered are likely to strain available budgets if attempted regionally and further obstacles would emerge from the public desire to maintain road access for traditional recreational and extractive activities (Trombulak & Frissell, 2000), preference of anglers for BKT and other non-native sport-fishes in some streams (Quist & Hubert, 2004), the need for public land agencies to manage for multiple uses rather than single species (Roper et al., 2018), and significant uncertainties about the rate and magnitude of future climate change (Wuebbles et al., 2017).

In the present conservation context for bull trout, thinking strategically is essential and understanding metapopulation characteristics pertinent to this species provides useful insights. We have demonstrated that proximity to an occupied natal patch is correlated with occupancy in nearby patches, which might be seen as evidence of metapopulation structure in bull trout. However, there are other valid interpretations (Rieman & Dunham, 2000; Schtickzelle & Quinn, 2007) and, rather than a discrete patch in which occupancy is dictated by extinction-colonization dynamics, it may be that home ranges of juvenile or stream-resident bull trout exceed the distances between the most proximal patches. In that case, the grain at which bull trout interact with their environment would make adjacent patches singular, size would be an even more dominant variable explaining occupancy, and mainland-island structure the most apt description. Regardless, our analyses suggest that the influence of neighboring patch occupancy declines beyond 10–20 km, a distance not atypical of home ranges of other resident salmonids (Young, 2011). This does not preclude metapopulation structure from developing at broader spatial scales, for which there is strong evidence from the hierarchical structure of genetic variation (Ardren et al., 2011). More problematic for viewing bull trout as forming classical metapopulations, however, may be the patterns of extinction and colonization. For example, there were losses of populations in many basins in the 20th century (which contributed to their listing under the Endangered Species Act) and more recent declines associated with the truncation of downstream portions of extant populations (Eby et al., 2014; LeMoine et al., 2020), yet almost no instances of recolonization beyond those fostered by assisted migration, and the status of many of these populations remain tenuous (Hayes & Banish, 2017). These dynamics are consistent with patterns in non-equilibrium metapopulations, that is, extirpations predominate in marginal or sink habitats and persistence depends on the stability and resilience of populations in large source habitats. That a small number of high-volume patches accounts for a markedly large proportion of currently occupied habitat further supports such an interpretation and also decreases the value of suitable but unoccupied patches, especially those that are small, because future climate change will most rapidly degrade their capacity to support populations.

The disproportionate importance of large patch habitats suggests they should serve as important anchor points in the development of local bull trout conservation strategies. Large patches are also the most resistant to change due to their size and may primarily require protection against degradation rather than new restoration investments. Toward this end, Williams et al. (2011) proposed the establishment of wild fish preserves that are formally recognized and protected for their intrinsic conservation value, a concept that is now backed by strong empirical evidence for bull trout. Around these large high-probability habitats, additional patches could be prioritized for restoration based on available resources, population occupancy status, and response potential to encourage the development of local enclaves where connectivity and dispersal among populations enhance overall resilience.

Restoration actions

The eradication of BKT populations from natal patch habitats can provide immediate and measurable benefits to sympatric bull trout populations through competitive release (Buktenica et al., 2013). However, such removals are usually limited to smaller patches that are more marginal habitats for bull trout and will require periodic surveillance to guard against reinvasions. New techniques involving the genetic swamping of BKT populations with sterile males could decrease costs and increase the extent of eradication efforts but their promise has yet to be demonstrated at broad scales (Kennedy et al., 2018; Schill et al., 2017). Road reduction efforts could benefit bull trout populations given the variety of mechanisms that are involved (Jones et al., 2000; Meredith et al., 2014; Trombulak & Frissell, 2000) and other distribution models have found that measures of human watershed impacts have generally negative influences on trout habitat occupancy (Dunham & Rieman, 1999; Peterson et al., 2014). Road density is often chosen to represent these impacts because of the availability of broad geospatial data sets and because road networks are often one of the few or only watershed alterations in remote mountain headwaters. Worth noting is that the expansion of the road network in our study area has been curtailed and road miles have even declined slightly in recent decades (Smith & McIlvain, 2018), so the negative effect on bull trout patch occupancy may largely represent a legacy effect from the previous century. Although remediation of road effects is feasible, the lengthy post-restoration timescales for stream habitat and fish populations responses could lag behind population losses from rapid climate change this century. Nonetheless, road removal efforts are increasingly undertaken by land management agencies and tools to identify and prioritize the subset of roads most harmful to streams that can be used to leverage these efforts (Al-Chokhachy, Black, et al., 2016; Black et al., 2012).

Our scenarios under-represented the beneficial effects that connectivity improvements could provide because we lacked comprehensive data to describe the locations of small anthropogenic barriers in headwaters and were limited to using information about larger dams and reservoirs. However, the S7 scenario simulating the disconnection of patches highlighted the importance of connectivity to maintaining higher occupancy rates based on the large drop in probabilities that was observed. Connectivity can be improved by provision of fish passage facilities at dams or water diversion structures, replacement of problematic culverts at road crossings, or the complete removal of these features, all of which have been the focus of ongoing and extensive restoration efforts in recent decades (Januchowski-Hartley et al., 2013; O'Connor et al., 2015; Roni et al., 2002). Connectivity might also be artificially enhanced through assisted migration into suitable habitats above geologic barriers if these areas have high probabilities of supporting resident populations. A recent effort to establish a refuge population in Glacier National Park was successfully accomplished by moving bull trout from a small downstream population that was being invaded by BKT into a historically fishless lake in the headwaters of the same drainage (Downs et al., 2015). Although sometimes controversial, oftentimes subject to low success rates (Hayes & Banish, 2017), and requiring coordination with conservation priorities for other species (Dunham et al., 2004), human-facilitated fish movements have a long tradition and are continuing the practice for species preservation at a time of rapid climate change warrants consideration.

Also of relevance are restoration tactics that attempt to decrease summer temperatures or increase discharge within bull trout natal habitats. These were not explicitly considered in our scenarios because hydroclimatic conditions were used to delimit patch habitats and changes to these conditions are the fundamental means by which climate change affects bull trout populations. Nonetheless, stream temperatures may be lowered in reaches that are heavily exposed to sunlight by increasing shade from riparian vegetation where it is significantly degraded (Justice et al., 2017; Nussle et al., 2015) although the effective scope of these actions will be limited to small patches or reach subsets within larger patches. Evidence of this is given by wildfires that often reduce shade across tens to hundreds of stream km, much larger extents than riparian vegetation restoration projects, yet still result in minor temperature changes compared with those associated with climatic variability (Holsinger et al., 2014; Isaak et al., 2010).

The large potential losses of future habitat highlighted by the volumetric patch size estimates suggest that tactics to maintain or improve summer baseflows will benefit bull trout populations. These might include acquisition of water rights or improved water use efficiency where streams are subject to water withdrawals for agricultural or residential purposes (Walters et al., 2013), actions which might also help to ameliorate temperature increases (Elmore et al., 2015). Reintroduction of beaver (*Castor canadensis*), which were once common throughout the northern Rocky Mountains and many bull trout streams, has gained attention for the potential effects on baseflows, meadow restoration, and diversification of stream habitats (Pilliod et al., 2018; Pollock et al., 2014). Beaver reintroductions or the use of beaver dam analogs are relatively inexpensive, could be used to treat many streams, and be targeted effectively using tools that highlight the best potential reintroduction sites (Macfarlane et al., 2017). Concerns exist that beaver ponds and complexes may slow stream velocities and increase temperatures but evidence suggests either minimal impacts or enhanced thermal diversity because hydraulic head pressure on the valley floor creates cold upwelling zones within a warmer overall matrix (Majerova et al., 2020; Weber et al., 2017). Most importantly from a habitat perspective, the wetted area available to fish and other organisms is often increased dramatically when single threaded streams are transformed into aquatic environments that fill valley bottoms (Bouwes et al., 2016; Hood & Bayley, 2008).

Key uncertainties

Adding to the challenges that habitat restoration efforts face are several key uncertainties. At the highest levels are those associated with the rate and magnitude of future climate change as manifest through air temperatures and precipitation regimes (Cox & Stephenson, 2007; Wuebbles et al., 2017), which will interact with topographic and geological features in headwater areas to elicit complex stream hydroclimatic responses. That regional and global trends in headwater streams are occurring is well established but substantial variability exists among streams, even within the same networks, that is not adequately captured by current models used to make broad-scale climate projections (Dugdale et al., 2017; Safeeq et al., 2014; Wenger et al., 2010). For our purposes, therefore, we made the simplifying assumption in the moderate and extreme climate change conditions that the increments of change would be identical across all streams while also not specifying the time frames over which these changes would occur. This sacrificed some realism by ignoring idiosyncratic responses of individual patch habitats but enabled a straightforward interpretation of results and risk assessment, while facilitating communication of our results to bull trout managers and decision makers.

If recent warming rates estimated at ~0.1°C/decade in the cold streams occupied by bull trout are maintained (Isaak et al., 2016), the thermal changes to natal patches in our climate conditions may not transpire for a century or more. However, these rates could increase if future climate forcing accelerates, or as snow-packs continue to decrease and the sensitivity of headwater streams increases (Leach & Moore, 2019; Luce et al., 2014). In the event of one or both of those changes, warming rates of mountain headwater streams may increase to align more closely with the faster rates observed historically in lower-elevation rivers and streams (Isaak, Luce, Horan, et al., 2018; Michel et al., 2020; Piccolroaz et al., 2018), and the projected changes in bull trout patches will happen sooner. Similar considerations apply to stream hydrology, where historical rates of summer flow declines within the study area have been 5%–10% per decade and cumulative decreases in the latter half of the 20th century were estimated at 25%–30% (Leppi et al., 2012; Luce & Holden, 2009). There is also an elevational gradient to flow declines, but one more problematic for bull trout because declines are larger at higher elevations where late spring and early summer snowmelt are important contributors to stream baseflows (Luce et al., 2013). The mechanisms contributing to these declines, and the degree to which they will persist in the future, remain subjects of debate and ongoing research, although there is little doubt that summer flows will continue to decline in streams of this snow-dependent region (Kormos et al., 2016; Luce et al., 2013; Mote et al., 2018).

On the biological side of the ledger, unknowns exist regarding future BKT distributions and the consequent effects on competition with bull trout. BKT, having a slightly warmer thermal niche, often occur downstream of the coldest headwater reaches occupied by bull trout (Isaak, Wenger, & Young, 2017; Rieman et al., 2006). When combined with a smaller average body size and shallower egg burial depths for BKT, these factors may combine to make their populations especially vulnerable to increases in winter flow variation where snow-to-rain hydrologic transitions occur (Wenger et al., 2011). Alternatively or simultaneously, continued stream warming may allow BKT distributions to expand upstream and enhance competitive pressures in the smaller streams preferred by this species (Warnock & Rasmussen, 2013; Wilcox et al., 2018). As a non-native species, there are also many potential habitats where BKT do not occur but which could be colonized, as evidenced by their occupancy of 56% of the bull trout patches (556 of 991) in our data set. However, current distributions of BKT appear strongly linked to historical patterns of stocking and road access, and colonizations of new streams rarely occur, except perhaps through illicit means involving angler transport (Dunham, Adams, et al., 2002, Dunham et al., 2004). The limited dispersal abilities of BKT may again relate to their small body sizes and possible difficulties navigating larger, warmer portions of river networks that link headwater patches.

Although the presence of or potential for an adfluvial life history was not a significant predictor of bull trout patch occupancy in our model, we acknowledge that residents and migrants may have somewhat different natal habitat preferences. The large size of most migratory fish (>400 mm; Mogen & Kaeding, 2005; Howell et al., 2016) would preclude them from occupying the smallest channels used by resident fish, which in turn appear to occupy channels larger than those acceptable to sympatric cutthroat trout (M. K. Young, unpublished data; Rich et al., 2003; Peterson et al., 2014). Despite calls for more information on the distribution, ecology, and demographics of resident bull trout (Dunham & Rieman, 1999; Rieman & Dunham, 2000), most research and monitoring continues to focus on fish exhibiting migratory life histories (Downs et al., 2006; Kovach et al., 2018; Nelson et al., 2002), and this lack of information may result in a biased perception of the status of particular bull trout populations. Moreover, although climate change may cause suitable natal habitat for both life history forms to decline, it may disproportionately affect migratory forms in four ways: (1) as a manifestation of the gill oxygen limitation hypothesis, in which warmer temperatures restrict the size of large fish because gill size does not increase linearly with fish mass (Meyer & Schill, 2021; Pauly & Cheung, 2018); (2) from temperature increases and wildfires enhancing productivity of high-elevation areas, leading to a reduction in upstream–downstream productivity gradients that favor migration (Ferguson et al., 2019; Finstad & Hein, 2012), (3) from greater losses of thermally suitable habitats in low elevation rivers and streams due to their faster warming rates and climate velocities (Isaak, Luce, Horan, et al., 2018; Isaak & Rieman, 2013), which increase the costs of migration (Bowerman et al., 2021; Mims et al., 2019), and (4) the continued spread in warmer areas of non-native piscivorous fish such as brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), northern pike (*Esox lucious*), and smallmouth bass (*Micropterus dolomieu*) that may dramatically reduce survival of juvenile bull trout migrants (Al-Chokhachy, Schmetterling, et al., 2016; Jalbert et al., 2021; Rubenson & Olden, 2020), the life stage parameter to which population growth is most sensitive in many demographic models (Al-Chokhachy & Budy, 2008; Budy et al., 2017; Howell et al., 2016). Consequently, bull trout population persistence may be less likely when migratory life histories are functionally obligate (e.g., in very low productivity natal habitats), and ignorance of resident life histories serves as a critical obstacle to gauging the status and potential trends of bull trout throughout its range.

The above factors are challenging to understand and predict in isolation but several will often act in concert and this synergy may ultimately pose the greatest threat to individual bull trout populations. The specifics of local population extinctions due to climate change are poorly understood for most species (Cahill et al., 2013; Durance & Ormerod, 2010) but, conceptually at least, involve changes in the mean or variance of environment conditions that interrupt normal population dynamics to a significant degree (Jackson et al., 2009). Juvenile growth and survival to maturity in salmonid fishes is sensitive to short-term (i.e., monthly to interannual) variability in hydroclimatic conditions (Clews et al., 2010; Copeland & Meyer, 2011; Crozier & Zabel, 2006), so a series of extreme floods or unprecedented multiyear droughts coupled with heat waves could severely test populations (Dai, 2013; Kanno et al., 2015), especially those in the smallest and most marginal habitats that may lack internal microrefugia (Sedell et al., 1990). Mass mortality events of cold-water species during warm temperature events are well documented (Hinch et al., 2012; Hutchins et al., 2021) but thus far confined to low elevation rivers where habitats are often near thermal maxima for species during warm months. Similar catastrophic effects could emerge in headwater areas, however, if stream intermittency becomes a more common occurrence in the future with summer flow declines (Kovach et al., 2019). Although wildfire prevalence did not appear in our final patch model and therefore lacked a consistent role in determining historical population occurrence at the patch scale, wildfire-related disturbances can cause local, reach-scale extirpations through immediate alterations of water physicochemical conditions (Hitt, 2003; Smith et al., 2011) or subsequent debris flow torrents (Bozek & Young, 1994; Dunham et al., 2007). A scenario could arise in which climate change systematically reduces the extent of bull trout natal habitats, which then become more vulnerable to wildfires which are growing in extent, frequency, and interactions with headwater networks (Alizadeh et al., 2021; Ball et al., 2021; Falke et al., 2015). Bull trout evolved with fire-related disturbance as a natural landscape element and populations often benefit from increases in habitat complexity and productivity that manifest over the longer term (Dunham, Young, et al., 2003; Luce et al., 2012; Sestrich et al., 2011). However, part of this resilience may stem from migratory life history types that recolonize affected reaches (Rieman, Lee, Chandler, et al., 1997), in which case a transition to more resident populations would exacerbate vulnerability.

Nonetheless, despite numerous studies, including our own, that invoke the threat of climate change to bull trout, we are unaware of any recent patch-scale population extirpations that can be unambiguously attributed to this phenomenon. In fact, the status of bull trout, apart from climate-induced shifts of downstream population boundaries (Eby et al., 2014; LeMoine et al., 2020) and declines in some fluvial and adfluvial populations (Howell et al., 2016; Nelson et al., 2002), appears to have stabilized in most areas since ESA listing in 1999 spurred widespread protective measures (Howell, 2018; Kovach et al., 2018; Meyer et al., 2014). In numerous instances, small populations that were first surveyed two or three decades ago (Buchanan et al., 1997; Nelson et al., 2002; Rieman et al., 2006) and recently resurveyed with eDNA, continue to persist in less than a kilometer or two of habitat (Young et al., 2017). Many of these populations are associated with local features such as lakes, springs, or extensive upwelling zones along valley profiles (Allen et al., 2010; Baxter & Hauer, 2000) and warrant additional study to understand their persistence. In some instances, headwater trout populations naturally isolated above geologic barriers can persist for hundreds or even thousands of years (Northcote, 2010; Whiteley et al., 2010) and lessons drawn from these unique populations may be instructive for bull trout conservation efforts. We caution, however, that some of these populations may represent "the living dead" and owe an extinction debt that has yet to be paid (Kuussaari et al., 2009). Only continued monitoring will determine whether our estimates of risk are realistic, or whether we have underestimated the resilience of bull trout, albeit perhaps only of the resident life history.

Model limitations

The final bull trout model correctly predicted patch occupancy 82.6% of the time, which we considered good performance for a large data set, especially one aggregated from multiple sources and sampling techniques. Future performance could be enhanced by continued improvements in geospatial covariates that, despite significant advances over the past decade, still possess inaccuracies. For example, the model used to develop the stream temperature scenarios had a spatial prediction error of 1°C (Isaak, Wenger, Peterson, et al., 2017) and the hydrologic model underlying the flow scenarios was least accurate in small streams because it is calibrated to data from gages that predominately occur on large rivers (DeWeber et al., 2014; Wenger et al., 2010). Representations of covariates based on remote sensing imagery such as wildfire prevalence and riparian conditions may be out of date or yet lack the resolution to resolve important attributes for fish populations (e.g., instream habitat complexity). In each of those cases, however, the data sets and capabilities of associated modeling or sensing platforms are improving and will translate to better habitat descriptions over time. The statistical significance of spatial factors such as HUC8 and easting coordinates in the patch occupancy model also implies that there are important determinants of patch occupancy for which covariate representations have yet to be intuited and developed. It is unclear what those determinants are, but future researchers could find utility by expanding our traditional patch-centric model to also incorporate the broader attributes of networks in which natal habitat patches are embedded. For example, the relatively simple distance-based connectivity metrics that we considered might be enhanced by accounting for landscape resistance (Luque et al., 2012) or factors explored that relate to enhanced growth opportunities in warmer environments downstream of natal areas (Armstrong et al., 2021).

Because habitat size is such an important factor in bull trout patch occupancy models (Dunham & Rieman, 1999; Rieman & McIntyre, 1995), we expended considerable effort to accurately characterize the extent of accessible reaches within natal patches through an editing process. However, the large network extent within patches (~16,000 stream km) and imperfect tools for performing this process (digital elevation models, the World Waterfall database, field observations) made it likely that areas accessible to fish were overestimated, although these errors would be skewed toward upstream patch extents where habitat volumes are small compared with downstream reaches. Another potential error source may relate to the use of old or incomplete biological survey information that incorrectly portrayed the status of bull trout occupancy or BKT prevalence in the modeling data set. Modern eDNA surveys, coupled with spatially extensive sampling designs (McKelvey et al., 2016; Young et al., 2017), can largely eliminate this uncertainty, but time and money are required to inventory large portions of species' ranges, meaning that older and less precise data sets will remain important resources for the foreseeable future despite their limitations.

CONCLUSION

During more than a decade contributing to studies focused at the nexus of climate change and the spatial ecology of bull trout (Isaak et al., 2010; Rieman et al., 2007), three things have become apparent. First, advances in the size and quality of data sets and stream models have added unprecedented precision to our ability to delineate and describe bull trout habitats across broad areas. Coarse watershed and elevation-based patch habitat descriptors have been improved by network-based models, hydroclimatic scenarios, and an array of stream habitat, land-use, and watershed descriptors that can be applied consistently throughout the species range to better characterize and assess the factors that affect population distributions. Second, despite these advances, uncertainty about the future of bull trout remains high within the context of a nonstationary climate. Key questions regarding future trends in stream habitats, biological elements and interactions among these factors exist and must be resolved to constructively address uncertainty, thereby highlighting the need for ongoing monitoring programs and a targeted research agenda. Third, bull trout continue to demonstrate marked resilience since the new stresses of climate change have been added to the traditional factors that caused widespread historical declines. This resilience buys valuable time, but is likely to reach its limits for some populations this century as environmental trends continue. Managers have at their disposal a suite of actions that can be undertaken to benefit bull trout, but need to be strategic about when and where those actions are taken to maximize effectiveness. The results of our modeling can serve as a guide to those actions and, by focusing available resources on and around large, well connected habitats with high probabilities of occupancy, the resilience of local population enclaves can be enhanced and the odds of long-term persistence maximized to help bull trout weather the uncertainties that lie ahead.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data sets and scenarios (Isaak et al., 2022) are available on Figshare at https://doi.org/10.6084/m9.figshare.19424033.v1.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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