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ARTICLE

Nonnative Trout Invasions Combined with Climate Change Threaten Persistence of Isolated Cutthroat Trout Populations in the Southern Rocky Mountains

James J. Roberts*
Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, Colorado 80523, USA; and U.S. Geological Survey, Colorado Water Science Center, 2150 Centre Avenue, Building C, Fort Collins, Colorado 80526, USA

Kurt D. Fausch
Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, Colorado 80523, USA

Mevin B. Hooten
U.S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Department of Fish, Wildlife, and Conservation Biology, Department of Statistics, Colorado State University, 1484 Campus Delivery, Fort Collins, Colorado 80523, USA

Douglas P. Peterson
U.S. Fish and Wildlife Service, Abernathy Fish Technology Center, 1440 Abernathy Creek Road, Longview, Washington 98632, USA

Abstract
Effective conservation of Cutthroat Trout *Oncorhynchus clarkii* lineages native to the Rocky Mountains will require estimating effects of multiple stressors and directing management toward the most important ones. Recent analyses have focused on the direct and indirect effects of a changing climate on contemporary ranges, which are much reduced from historic ranges owing to past habitat loss and nonnative trout invasions. However, nonnative trout continue to invade Cutthroat Trout populations in the southern Rocky Mountains. Despite management to isolate and protect these native populations, nonnatives still surmount barriers or are illegally stocked above them. We used data on the incidence of invasions by nonnative Brook Trout (BT) *Salvelinus fontinalis* and the rate of their invasion upstream to simulate effects on a set of 309 conservation populations of Colorado River Cutthroat Trout (CRCT) *O. c. pleuriticus* isolated in headwater stream fragments. A previously developed Bayesian network model was used to compare direct and indirect effects of climate change (CC) alone on population persistence versus the added effects of BT invasions. Although CC alone is predicted to extirpate only one CRCT population by 2080, BT invasions and CC together are predicted to completely extirpate 122 populations (39% of the total) if managers do not intervene. Another 113 populations (37%) will be at risk of extirpation after CC and invasions, primarily owing to stochastic risks in short stream fragments that are similar under CC alone. Overall, invasions and CC will reduce the number of stream fragments that are long enough to buffer CRCT populations against negative genetic consequences and stochastic disturbances by 48, a decrease of 38% compared to CC alone. High priorities are (1) research to estimate how CC and human factors alter the incidence and rate of BT invasions and (2) management to prevent new illegal introductions, repair inadequate barriers, and monitor and address new invasions.

*Corresponding author: jroberts@usgs.gov
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Conserving native trout requires understanding their ecological relationships at a hierarchy of scales from stream reaches to river basins and managing for regional persistence in the face of multiple stressors. The principal stressors that have caused native trout declines in many regions over the last 150 years are loss of habitat from human land uses and water abstraction, as well as invasions by nonnative trout (Young 1995; Kitano 2004; Hudy et al. 2008). Overlain on these stressors in recent decades has been the influence of climate change, which includes direct effects on water temperatures and stream flows and indirect effects ranging from habitat fragmentation to altered hydrologic regimes (Rahel and Olden 2008; Wenger et al. 2011; Isaak et al. 2012). Effective conservation of native trout will require planning for a future that includes all these factors and taking actions that are both targeted at the most important stressors and effective at ameliorating them (Fausch et al. 2009; Isaak et al. 2015).

One group of native trout for which these multiple stressors pose strong threats are the lineages of Cutthroat Trout *Oncorhynchus clarkii* in the southern Rocky Mountains (Behnke 1992; Metcalf et al. 2012). In this region, the remaining populations are restricted to short headwater stream fragments (often less than 6 km long) by previous habitat loss and invasions by nonnative trout (Harig et al. 2000; Alves et al. 2008; Hirsch et al. 2013). Our recent analysis for 309 conservation populations that remain of the most widespread subspecies, the Colorado River Cutthroat Trout *O. c. pleuriticus* (CRCT), predicted that the majority of these small populations (63%) are susceptible to extirpation by stochastic disturbance events such as wildfire, sediment debris flows, drying, and freezing, events which are predicted to increase in frequency with climate change (Roberts et al. 2013). In contrast, few of these populations are susceptible to extirpation by future temperature increases alone because nearly all are located in high-elevation headwater streams that are predicted to be either within optimum temperature limits for reproduction and growth or too cold despite the changing climate.

Most Cutthroat Trout populations in the southern Rocky Mountains are also protected from upstream invasions by natural or artificial barriers that form their downstream limit (Young et al. 2002; Pritchard and Cowley 2006; Young 2008). Nevertheless, invasions are a regular occurrence, either because barriers are ineffective or fail (Thompson and Rahel 1998; Harig et al. 2000), or humans deliberately move trout above them (Fausch et al. 2009). These nonnative trout can rapidly colonize upstream (Peterson and Fausch 2003), further reducing the length of stream fragments available to support the native trout, and often extirpate Cutthroat Trout within about a decade from many small streams (Peterson et al. 2004, 2008).

Broad-scale analyses of climate change effects on native Cutthroat Trout (Williams et al. 2009) and the effects of climate change combined with nonnative trout (Wenger et al. 2011; Isaak et al. 2015) have been conducted for the Rocky Mountain region. However, most analyses to date used air temperature as a surrogate for water temperature when predicting future conditions, and all have used broad-scale species distribution models to predict suitable habitats for native and nonnative trout, making it difficult to identify effects at local scales. In contrast, to be effective for managing the small, restricted Cutthroat Trout populations that remain in the southern Rocky Mountains, analyses will need to account for the unique attributes of the native trout lineages and nonnative trout invasions in the region, and water temperatures and fragment lengths in the specific streams that support conservation populations. Toward that end, our goal was to analyze the combined effect of invasions by nonnative trout and the direct and indirect effects of climate change for the 309 conservation populations of native CRCT throughout the upper Colorado River basin. We ask how important are potential nonnative trout invasions above barriers when combined with the effects of climate change in extirpating native trout and reducing persistence of the remaining populations. Lastly, we consider what management actions are likely to be most effective at ameliorating threats from these multiple stressors to native Cutthroat Trout populations in the southern Rocky Mountains.

METHODS

CRCT population database.—We used the CRCT Conservation Team database to map the distribution and status of CRCT populations on the landscape (Hirsch et al. 2006; Figure 1). This database combines all available population surveys from management agencies (state, federal, and tribal) and university researchers to specify which stream segments in the National Hydrography Dataset Plus (NHDPlus; 1:100,000; http://www.horizonsystems.com/nhdplus) are occupied by CRCT populations, and their conservation status. We restricted our analysis to CRCT conservation populations, defined as those with ≥90% genetic purity. Most conservation populations were also isolated from nonnative trout invasion by barriers or unsuitable habitat, and free from disease (Hirsch et al. 2006, 2013). We used the same 309 populations analyzed in previous work (Roberts et al. 2013) to allow comparing the effects of climate change alone and combined with nonnative trout invasion. This was the set included in the most current database available in 2009 when we began our previous research.

Incidence of nonnative trout invasion.—We restricted our analysis to invasions by Brook Trout *Salvelinus fontinalis* (BT) because it is the most common nonnative trout directly downstream from the barriers that isolate CRCT populations in the Colorado River basin (Fausch 1989; Young 1995), and extirpation of CRCT populations after BT invasions is well-documented (Peterson et al. 2004, 2008; Young 2008). Other nonnative trout such as Rainbow Trout *O. mykiss* and Brown Trout *Salmo trutta* tend to occur farther downstream, so they invade habitat occupied by CRCT less frequently, except when stocked there.

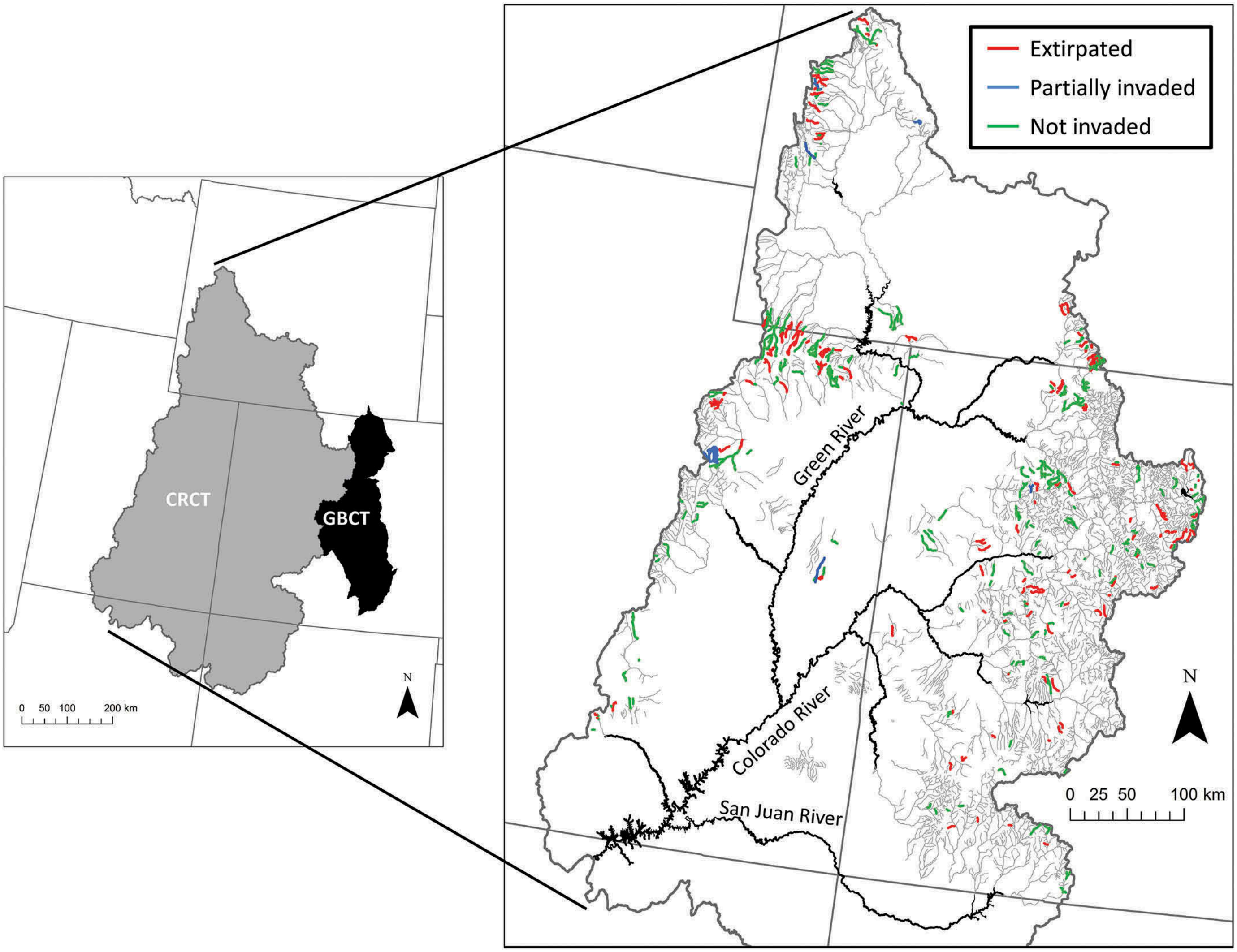

FIGURE 1. Map of the 309 conservation populations of Colorado River Cutthroat Trout (CRCT) showing one randomly chosen simulation (number 57) of invasion by Brook Trout (BT) in 2080, after seven decades. Stream segments were either invaded and completely extirpated by BT (N = 134), only partially invaded so that a CRCT population is still predicted to occur in the portion not invaded (N = 6), or not invaded (N = 169). Rivers historically occupied but currently unoccupied by CRCT are represented by gray lines, and major rivers and reservoirs of the Upper Colorado River basin are shown in black. The inset shows the upper Colorado River basin, which includes the native range for CRCT, and the South Platte and Arkansas River basins, which were originally considered the native range for Greenback Cutthroat Trout (GBCT).

Because there are no data sets on the incidence of invasions by BT into CRCT populations, we used data for Greenback Cutthroat Trout *O. c. stomias* (GBCT; see Figure 1 for native range) as a surrogate. Similar to CRCT, GBCT are found only in small stream fragments (median length 2.48 km) at high elevation. Invasions into GBCT populations have been consistently monitored and documented since the discovery of a few remnant populations in 1965 and federal listing under the Endangered Species Act (Endangered Species Act of 1973; Harig et al. 2000), so we judged that these data provide the best estimate of the incidence of BT invasions into native Cutthroat Trout populations in the southern Rocky Mountains. The rates are likely to be similar among the extant subspecies in the southern Rocky Mountains because all are ecologically similar, having diverged only during or since the last glacial period (Behnke 1992, 2002).

We estimated the incidence of BT invasion into GBCT populations by evaluating the fate of historical and translocated populations over a 40-year period from 1965 to 2005. Recovery efforts for GBCT included searching for undiscovered pure populations and translocation of trout propagated from these pure populations into headwater streams above barriers, either those that were fishless or after nonnative trout were removed using piscicides (Young and Harig 2001). Translocations stopped after 2005 for almost a decade owing to concerns over whirling disease and the identity of lineages used for translocations (Metcalf et al. 2007, 2012).

We evaluated the fate of the 14 historical GBCT populations eventually discovered, and 29 translocations from these that established reproducing populations, based on detailed reports of the U.S. Fish and Wildlife Service (USFWS) recovery efforts, supplemented by personal communication with fishery biologists (USFWS 1977, 1983, 1993; Young et al. 2002). These reports allowed us to separate populations that remained uninvaded during each decade from those that were invaded, and exclude those where incomplete removal allowed the remaining BT to reproduce and recolonize (e.g., age-0 BT were found far upstream from the barrier soon after treatment with piscicides). Like the CRCT populations, nearly all of the GBCT populations are bounded downstream by barriers or unsuitable habitat and have populations of BT downstream (Young et al. 2002). Moreover, recent genetic evidence showed that all but one population of GBCT tested to date were actually two lineages of CRCT (Metcalf et al. 2012), owing to early stocking that established CRCT populations within the GBCT range that were then considered native and pure. Therefore, the incidence of BT invasion into these Cutthroat Trout populations is an excellent surrogate for modeling the future fates of CRCT conservation populations.

Analysis of these data showed that, on average, about 8% of the populations considered to be GBCT were invaded per decade (Table 1). This rate assumes that the populations available to be invaded each decade included (1) all noninvaded historical populations ever discovered, and (2) all translocated populations that had established reproducing populations by the beginning of the decade and were not invaded. Over the 40-year period, 9 of 43 viable populations were invaded.

*Rates of upstream invasion.—*After a Cutthroat Trout population is invaded, BT rapidly colonize upstream habitat (Peterson et al. 2004). Invading BT moved upstream primarily during summer at a mean rate of 15.3 m/d, based on median rates measured over two summers in three streams with CRCT populations (Peterson and Fausch 2003: range, 9.0–25.0 m/d across streams, for 405 BT marked and recaptured within a summer). Expanding these rates for a 100-d summer leads to an estimated median rate for upstream invasion of 1.53 km/summer. In long segments of two other streams in the same region that were already completely invaded by BT, Gowan and Fausch (1996) found that BT moved upstream more often than downstream during summer (i.e., July through September) and at a similar rate, 16.8 m/d. These results corroborate those of Peterson and Fausch (2003) and indicate that when BT surmount barriers or are introduced above them, they will attempt to move upstream and can invade 46 km of habitat over a three-decade period.

Brook Trout are likely to establish reproducing populations after initial invasion in headwater streams of the southern Rocky Mountains, and these populations, coupled with constant immigration from downstream source populations, are known to extirpate Cutthroat Trout. Brook Trout are better preadapted for the snowmelt runoff flow regimes than are Cutthroat Trout, owing to the evolutionary history of each species (Fausch 2008), and can recruit in the colder temperature regimes of headwater streams that suppress or eliminate Cutthroat Trout recruitment (Harig and Fausch 2002; Coleman and Fausch 2007a, 2007b). Results of a 4-year large-scale field experiment in four streams showed that invading BT strongly reduced survival of age-0 and age-1 Cutthroat Trout (Peterson et al. 2004), and stochastic simulations using a stage-structured matrix population model based on empirical estimates from this experiment showed that median extinction time for Cutthroat Trout populations subject to Brook Trout invasion is 10 years (95% confidence interval [CI]: 7–12 years). However, these results are based on relatively few streams, and data on the rates of BT invasion and establishment, including the extirpation of Cutthroat Trout in response, have not been compiled or analyzed across their entire range in the southern Rocky Mountains. Nevertheless, there is no evidence of Cutthroat Trout populations that have persisted for more than a few decades after BT invasion in this region (Kevin Rogers, Colorado Parks and Wildlife, personal communication), indicating that extirpation following invasion is likely under most conditions.

TABLE 1. Incidence of invasion by Brook Trout into Greenback Cutthroat Trout populations during four decades. Historical populations discovered in each decade are shown, as are reproducing populations established by translocating genetically pure fish to new streams. The cumulative number of these translocations that were not invaded, and were therefore available for invasion, are also shown for each decade. The incidence of invasion in each decade is the number of populations invaded, divided by the sum of all historical populations discovered (N = 14) and the cumulative number of translocated populations available for invasion in that decade.

Time period	Historical populations discovered	Populations established by translocation	Translocated populations available for invasion	Populations invaded	Incidence of invasion (% per decade)
1965–1974	7	3	3	2	11.7
1975–1984	2	10	11	2	8.0
1985–1994	3	12	21	3	8.5
1995–2005	2	4	22	2	5.5
Totals	14	29		9	Mean = 8.4

*Simulations of invasions across CRCT populations.—*To assess the threat of nonnative BT invasion into CRCT populations and the resulting loss of stream fragment length, we used annual time steps from 2010 to 2080 (a 70-year time horizon) and simulated the CRCT populations to be invaded each year as random variables arising from a Bernoulli probability distribution (i.e., a random binomial distribution) with the parameter equal to 0.008 (i.e., 0.8% of populations invaded per year), or one tenth of the decadal rate of 8% (Table 1). Populations that were invaded were no longer available for invasion, to mimic the natural process whereby additional BT invasions into these CRCT populations cannot be detected. For invaded populations, we then reduced fragment length by 1.53 km/year until the invasion was complete (i.e., all available CRCT habitat was occupied by BT) or the simulation reached the endpoint at 2080. Populations that were not completely invaded by 2080 are termed fragmented, where CRCT are largely allopatric in the fragment not invaded by BT. Because BT rapidly replace native Cutthroat Trout in streams of this region, we assumed that CRCT would be extirpated from each invaded segment within a decade. We performed 100 rangewide simulations of this invasion process using the statistical package R 3.3.1 (R Development Core Team, Vienna).

*Prediction of stream temperatures and persistence of populations.—*In summary, mean water temperatures in uninvaded stream fragments with allopatric CRCT populations were predicted for a current decade and for two future time horizons from dynamically downscaled climate projections (Hostetler et al. 2011; Represented Concentration Pathways 8.5 emissions scenario), and persistence of these populations after BT invasion was predicted from a Bayesian network model (Figure 2). Most methods and models were presented in Roberts et al. (2013; see also its Supporting Information for details) and are described briefly here.

Two metrics of water temperature that affect Cutthroat Trout survival and growth were predicted from stream temperature models: the average daily maximum temperature for the warmest week (MWMT), which affects survival, and the average daily water temperature for the warmest month (M30AT), which affects recruitment and growth. The models were developed from water temperature records for 274 sites throughout the Colorado River basin. The final temperature models predicted these two metrics from seven covariates: air temperature and summer discharge at the nearest available monitoring sites (both predicted from a dynamically downscaled regional climate model), latitude, drainage area,

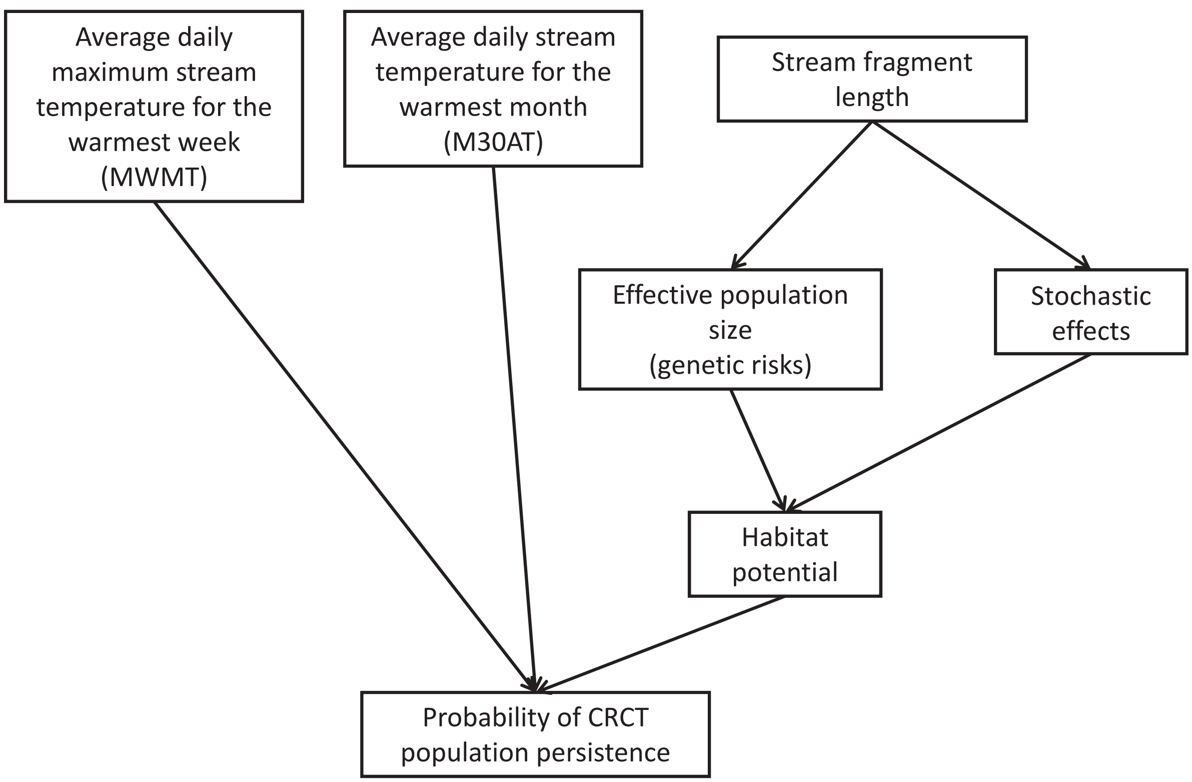

FIGURE 2. Simplified directed acyclic graph of the Bayesian network model (after Roberts et al. 2013) used to estimate probability of persistence for 309 isolated populations of native Colorado River Cutthroat Trout (CRCT) populations, given Brook Trout invasions and increasing temperatures projected under a changing climate. Boxes represent important factors that influence the probability of persistence for CRCT populations and arrows represent influences among factors. The probability of persistence for the current period and two future time horizons (2040 and 2080) is predicted based on (1) modeled water temperature in each stream segment that influences survival, growth, and recruitment; and (2) stream fragment length that influences the probability of genetic risks from small population sizes and the risk that stochastic events such as freezing, drying, or debris flows can extirpate populations in short stream fragments.

elevation, slope, and aspect. Each metric was predicted for each NHDPlus segment that made up the uninvaded habitat for each Cutthroat Trout population for a current decade (mean for 2000–2009), for 2040 (2035–2045), and for 2080 (2075–2085), and the results were averaged across segments for each time horizon to determine the thermal conditions for each population.

Predicted water temperatures for current conditions, the 2040s, and the 2080s were used as inputs to the Bayesian network model that predicts the probability of persistence for CRCT populations from the two temperature metrics and stream fragment length (Figure 2; see Roberts et al. 2013 and its Supporting Information for details and references). In this model, persistence is influenced by four main factors. First, maximum temperatures (i.e., MWMT) that are too high can kill CRCT, and high average daily temperatures (M30AT) can reduce their growth. Second, in contrast, average daily summer temperatures that remain too low reduce recruitment of CRCT fry. Third, stream fragment length influences fish abundance and effective population size. Longer fragments support more fish, which increases genetic diversity and the ability of small populations to adapt and persist under changing environmental conditions. Fourth, longer stream fragments also provide refuges from stochastic disturbances such as wildfire, debris flows, and stream drying and freezing. This information was incorporated in the Bayesian network model and conditional probabilities were estimated for the effect of each factor (shown as arrows in Figure 2) on other factors and on population persistence. The Bayesian network was developed and analyzed using Netica 4.16 (Norsys Software Corp., Vancouver, British Columbia, Canada).

For the analysis reported here, the lengths of stream fragments that remained uninvaded by BT for each CRCT population at 2040 and 2080 from each of the 100 stochastic simulations were used as inputs for the Bayesian network model (Figure 2), along with the two predicted stream temperature metrics for each uninvaded fragment. This resulted in 100 separate predictions of population persistence for each of the 309 populations at each time horizon. Populations that were completely invaded were assumed to be extirpated. Results were summarized to show the distributions of both uninvaded fragment lengths at each time horizon and mean predicted probabilities of persistence for the entire set of CRCT populations. We followed the definition of population vulnerability used by the International Union for Conservation of Nature, whereby a population is considered vulnerable if it has <90% probability of persistence over the next 100 years (Mace and Lande 1991). We defined populations that fell in this category by the 2080 time horizon of this analysis as "at risk of extirpation."

Sensitivity of CRCT extirpations to the incidence and rate of BT invasion.—Many factors may affect the incidence and rate of BT invasion in the southern Rocky Mountains, including distance to roads or trails that provide access for illegal introductions and effects of changing temperature regimes on BT upstream movement or establishment. Unfortunately, no data are available on how these factors affect the incidence or rate, so we had no basis for including them in our simulations. To address this problem, we conducted a sensitivity analysis to assess potential effects of factors that alter these two primary drivers of extirpation of native Cutthroat Trout populations via BT invasion and to determine which driver has the greater effect.

Managers can attempt to reduce risk to populations of CRCT shortened by BT invasion by building barriers and removing nonnative trout to increase fragment length and number of Cutthroat Trout, or perhaps by managing riparian habitat to alter thermal regimes (Lawrence et al. 2014) so that temperatures would favor CRCT. However, CRCT populations that are extirpated completely are difficult to reestablish (Harig and Fausch 2002), because the locally adapted population is lost. In addition, removing BT from even short fragments is time consuming and expensive (Shepard et al. 2002) and is not always successful (Meyer et al. 2006). Therefore, the response variable we selected for our sensitivity analysis is the total number of extirpated CRCT populations after 70 years, in 2080. We varied the incidence and rate of BT invasion from less than half (<–50%) of the original value used in the model to more than twice that value (+100%). Thus, we varied the incidence of invasion from 0.1 to 1.6%/year, and the rate of upstream invasion from 0.5 to 4.0 km/year. Although we know nothing about the variability of the incidence of invasion, the range of the median rates of invasion in the three streams over 2 years was 0.9–3.3 km/year (Peterson and Fausch 2003).

For this sensitivity analysis, we held one of the two variables constant at the original value and varied the other over the entire range of values selected, conducting 100 simulations as before. We then recorded the number of CRCT populations for which the fragment length was reduced to zero, indicating extirpation.

RESULTS

Our simulations show that many of the 309 conservation populations of CRCT are predicted to be completely invaded by BT and extirpated. Although estimates from the Bayesian network show that under climate change only one population would be extirpated by 2080 (i.e., 0% probability of persistence) from rising temperatures and stochastic events, given current habitat fragmentation, these threats combined with BT invasion would cause 52 populations to be lost by 2040 (17% of the total) and 122 by 2080 (39%).

Invasion by BT moved a large proportion of CRCT populations into the category of stream fragments that have limited buffering from stochastic environmental disturbances, and in which populations are faced with negative genetic consequences owing to low abundance (i.e., <3.6 km; see Roberts et al. 2013 for complete criteria). The median length of stream fragments, including those extirpated, was reduced from the current length of 5.9 km to 4.4 km in 2040 and to only 2.3 km by 2080 (Figure 3). Most important is that the loss of stream habitat to invasions reduced the number of fragments that provide robust buffering to populations (>7.2 km) from 125 currently to only 77 in 2080, a 38% decrease. A map showing the spatial distribution of the BT invasions for one of the simulations indicates that they occurred throughout the basin with no apparent pattern, as intended (Figure 1). However, in 2080 relatively few of the populations were only partially invaded (only six in this simulation), because in streams where BT do invade they proceed upstream quickly and are predicted to rapidly extirpate populations of CRCT in the relatively short stream fragments where they now occur.

The effects of BT invasion combined with climate change imperil many more populations than climate change alone, and these populations fall into three groups. First, invasions are predicted to extirpate 122 populations by 2080, including many of the 190 that would be placed at risk by climate change alone (Figure 4). Second, another 113 populations that are not extirpated by 2080 are predicted to be at risk of extirpation (<90% probability of persistence) by the combination of changing water temperatures and stochastic environmental events. Third, of this total, a small number of populations (5 on average; range, 1–11) are placed at risk because invasions shortened the fragment inhabited by CRCT. Overall, the total of 235 populations extirpated or placed at risk by invasions and climate change by 2080 represents 76% of all the conservation populations, a 24% increase over the 190 populations extirpated or placed at risk by climate change alone.

In the sensitivity analysis, varying the incidence of BT invasion had a large effect on the number of CRCT populations extirpated by 2080, whereas varying the rate of upstream invasion had little effect. For example, reducing the incidence by half resulted in a 43% decrease in the number of populations extirpated, and doubling the rate increased it by 64% (Figure 5). In contrast, reducing the rate of upstream invasion to a third resulted in only a 15% decrease in extirpations, and doubling the rate of upstream invasion increased extirpations by only 4%.

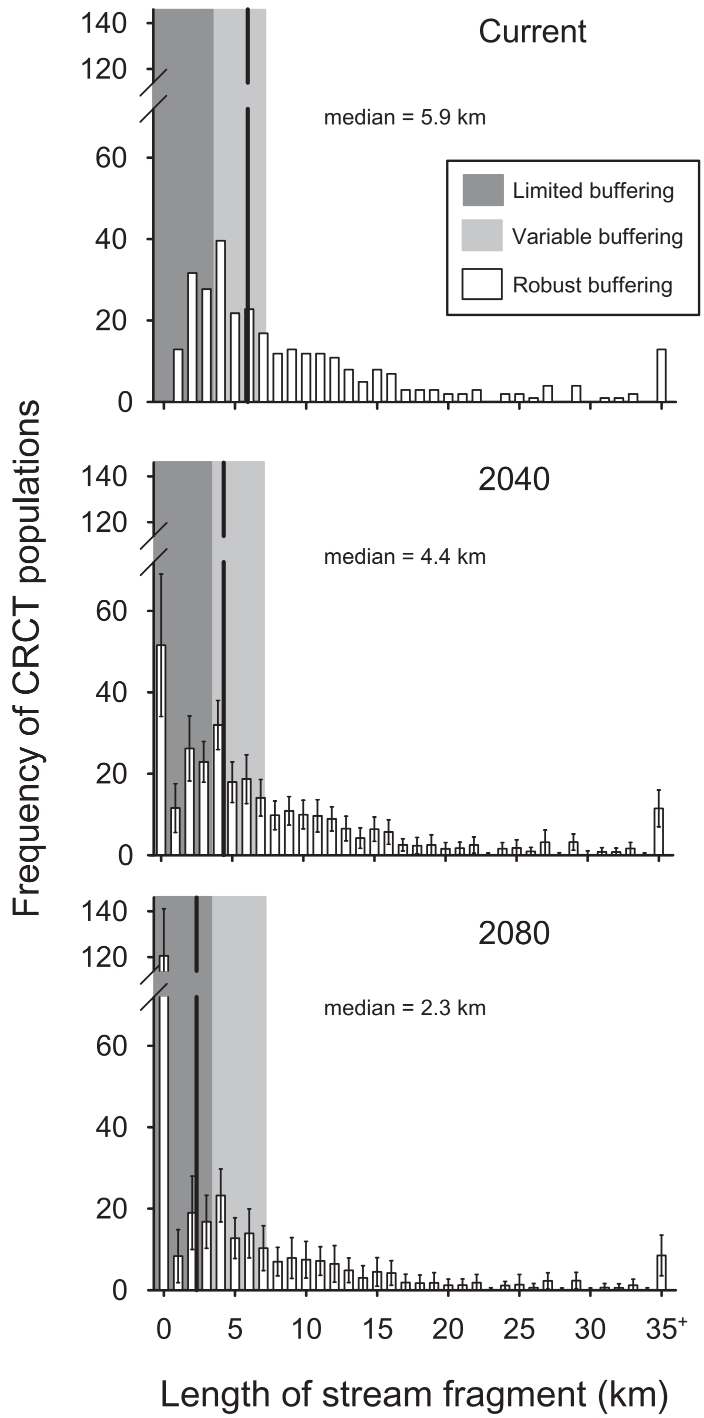

FIGURE 3. Frequency of lengths of stream fragments that support Colorado River Cutthroat Trout (CRCT) conservation populations in their current state (Current) and after simulations of three decades (2040) and seven decades (2080) of invasions by Brook Trout. Bars show mean and range of frequency in 1-km bins. The bars labeled zero include all fragments completely invaded by Brook Trout for the two future periods. Shading shows thresholds of fragment length that provide robust buffering from stochastic environmental events (no shading; >7.2 km), variable buffering (light gray; 3.6–7.2 km), and limited buffering to these events (dark gray; <3.6 km). The thick black line shows the median fragment length at each time horizon.

DISCUSSION

Our analysis shows the necessity of including the full range of important stressors in a given region when estimating persistence for native trout across their ranges. Adding predicted future invasions by nonnative BT to climate change–induced threats (i.e., effects of altered temperature and increased frequency of stochastic events) resulted in an estimate of 121 more populations being extirpated (122 total, 39% of all 309 populations) and 113 populations at risk of extirpation (37% with a less than 90% probability of persistence) by 2080. Moreover, we predict a substantial reduction of the

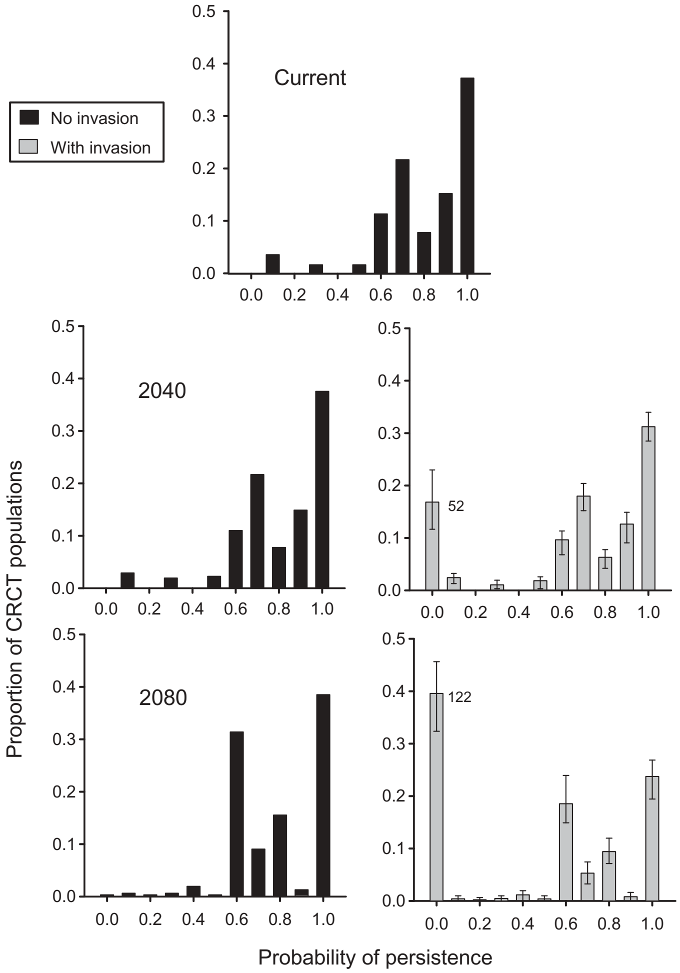

FIGURE 4. Frequency histograms of the probability of persistence for 309 Colorado River Cutthroat Trout (CRCT) conservation populations under current conditions and at two future time horizons (2040 and 2080). For these future periods, the left panels (black) show the effects of climate change and past fragmentation, whereas the right panels (gray) also include the predicted invasion by Brook Trout that reduces fragment lengths (bars show mean and range across all simulations). For the scenario that includes invasions, the bins labeled zero show the proportion and number of populations completely invaded and extirpated by Brook Trout.

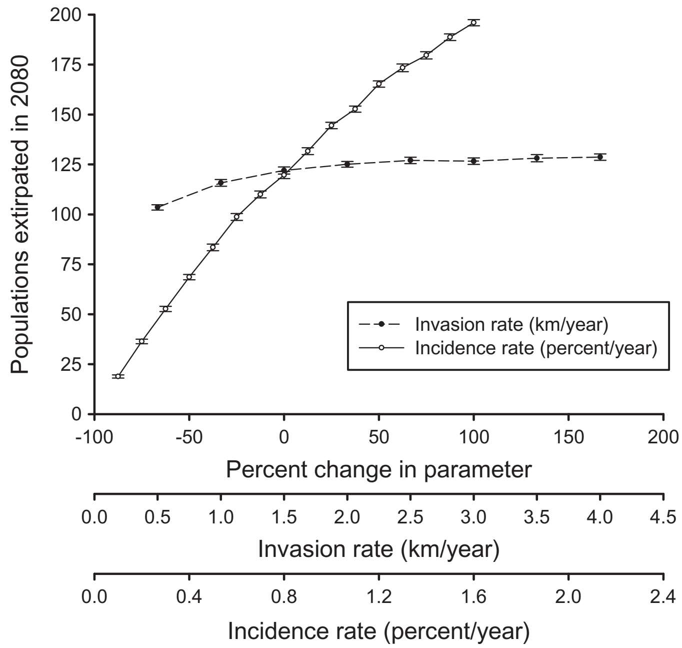

FIGURE 5. The effect of changing the incidence of Brook Trout invasions, and the upstream rate of invasions, on the number of Colorado River Cutthroat Trout populations extirpated in 2080. Points show the mean of 100 simulations of each rate (bars show 95% CI), holding the other variable constant at the original value. The main *x*-axis shows the percent change in the parameter varied in the simulation, and the two lower *x*-axes show the values of each rate.

largest CRCT populations, those in stream fragments long enough to be robust to stochastic environmental events owing to sufficient habitat length (>7.2 km) and robust to potential negative genetic consequences owing to sufficient population sizes (>7.7 km; see Roberts et al. 2013 for derivation of these thresholds). In all, BT invasions are predicted to shorten stream fragments that support 48 of these large robust populations below these thresholds, or in most cases extirpate the populations entirely, which is nearly a 40% loss from this category of large conservation populations. In the final analysis using the Bayesian network to estimate probability of persistence, adding the effects of BT invasion resulted in 45 more populations being placed at risk (<90% persistence) or extirpated by 2080, totaling more than three quarters of all conservation populations. This represents a 24% increase over the number at risk under climate change alone (235 versus 190 populations). However, this statistic underestimates the effect of BT because a majority of CRCT populations at risk are extirpated altogether (122 populations) when BT invasions are included.

The important stressors for native Cutthroat Trout in the southern Rocky Mountains and their effects on population persistence are likely to differ from those predicted for other regions, such as the northern Rocky Mountains. In the northern region, BT invasion is expected to be reduced with climate change as habitat become less suitable, owing to a combination of increases in temperature and winter rain regimes that scour eggs from redds of these fall-spawning char (Wenger et al. 2011). In contrast, the warmer water temperatures and lower spring precipitation caused by climate change in that region have increased upstream invasion by Rainbow Trout, resulting in hybridization that is extirpating pure populations of Westslope Cutthroat Trout *O. c. lewisi* (Muhlfeld et al. 2014; but see McKelvey et al. 2016). However, in the southern Rocky Mountains, invasions by Rainbow Trout into CRCT populations are less common because the upstream limit for this nonnative species is usually near the downstream limit of BT, so Rainbow Trout are not commonly found near the cold headwaters where CRCT occur. In the northern Rocky Mountains, native Cutthroat Trout still maintain populations in larger stream networks that extend to lower elevations. As a result, increased water temperature at these lower elevations is predicted to be the primary driver of a 58% decline in length of suitable habitat for Cutthroat Trout throughout the Rocky Mountains by 2080, most of which will occur in the northern region (Wenger et al. 2011). These differences in key drivers underscore the importance of developing models at regional scales for particular trout lineages and ecological settings to ensure accurate predictions and effective management.

The analysis we present here is straightforward and includes important stressors, but does not account for other interactions that could alter outcomes of invasions or population persistence. For example, changes in temperature or flow regimes may alter BT invasions by altering outcomes of biotic interactions (DeStaso and Rahel 1994; but see Novinger 2000), or rates of individual growth (Al-Chokhachy et al. 2013), population growth (Al-Chokhachy et al. 2016), or upstream movement. Nevertheless, several lines of evidence suggest that our results may be conservative. First, we used median rates for invasions, yet dispersal kernels for BT are most often leptokurtic with some long-distance migrants (Peterson and Fausch 2003; Pepino et al. 2012), and this jump dispersal is likely to drive invasion rates even higher than we estimated (Kot et al. 1996; Lewis 1997). Second, projections for the southern Rocky Mountains—earlier snowmelt and drying of streams with climate change (Clow 2010; Isaak et al. 2012)—will likely cause more stream drying and freezing in headwater reaches, reducing fragment size more than we predicted. Third, BT populations are likely to be more robust than Cutthroat Trout to many environmental changes predicted for these streams (e.g., increased temperature, lower flows), except for a change to a winter rain flow regime (Fausch 2008). However, a change in the flow regime this drastic is unlikely in southern Rocky Mountain high-elevation streams, which are expected to remain dominated by melting snow (Fritze et al. 2011; Gao et al. 2011). To resolve these and other uncertainties, we suggest that future research focus on gathering better empirical data and fitting predictive models to address three key topics: (1) how BT invasion rates vary with temperature, flow, and the presence of lakes and other geomorphic features; (2) current and future flow regimes and their influence on native and nonnative trout populations; and (3) how the incidence of BT invasion varies with distance to roads and other nodes of human influence.

Although uncertainty about how these added factors affect BT invasions prevented us from including them in our model, our sensitivity analysis showed that rangewide extirpations of CRCT populations will be affected much more by factors influencing the incidence of invasion than the rate of upstream invasion. For example, extirpations could be reduced by nearly half if managers found ways to reduce incidence by half, perhaps by fortifying barriers and developing educational campaigns that reduced illegal introductions. In contrast, even rates of invasion of 0.5 km/year, which is only about half of the lowest value measured in the field (0.9 km/year), resulted in extirpations at 85% of the value we estimated for the original rate. These rapid rates of upstream invasion emphasize the need to prevent invasions and to monitor and detect them early before BT begin spreading.

Our results also do not account for intervention by managers but do support ongoing management strategies and point to further actions that could be considered. Populations of CRCT are actively managed (Hirsch et al. 2013), and conservation biologists are unlikely to stand by as populations are extirpated by either invasions or the effects of climate change. For remnant populations of native salmonids where the degree of invasion threat is high, a strategic decision model proposed by Fausch et al. (2006, 2009) calls for selecting replicate fragments of optimum size and isolating them with barriers, removing invaders, restoring habitat quality, and translocating pure native trout to start new populations (see also Rahel 2013). In addition to seeking undiscovered pure populations, these are the management strategies that have been pursued by the CRCT Conservation Team and are planned for the future (Colorado River Cutthroat Trout Coordination Team 2006; Hirsch et al. 2013). Although there is heightened concern about the impending effects of a changing climate on temperature, flow regimes, and the frequency of stochastic events on CRCT fragments, our results indicate that high priorities for management should also continue to be preventing new illegal introductions of BT, repairing barriers that are inadequate, and monitoring for new invasions. Kondratieff and Myrick (2006) developed a model to evaluate barriers for risk of breach by BT ascending upstream, allowing managers to determine which barriers provide inadequate protection and require modification. Likewise, fragments should be monitored regularly upstream of barriers to detect invasions early, especially in areas of frequent human activity. Finally, educating the public about the danger of illegal introductions, taking steps to prevent them, and reducing the number of fish introduced (termed propagule pressure) are the most effective and least expensive ways to limit invasions (Fausch and García-Berthou 2013), far more so than attempting to eradicate or control ongoing invasions (e.g., Meyer et al. 2006; Buktenica et al. 2013; Pacas and Taylor 2015).

When invasions do occur, our models allow managers to weigh a range of options. For example, when a BT invasion is detected, the Bayesian network model (Roberts et al. 2013) can be used first to determine if building a new barrier that isolates the remaining CRCT upstream in a fragment of specific length and temperature characteristics would allow maintaining population persistence above or equal to a 90% probability for a given future time horizon (e.g., 30 years). If this is the case, then managers would also have time to build barriers farther downstream, remove the invaders in between, and thereby increase fragment length to further promote population resilience (Fausch et al. 2009). Second, if a fragment is completely invaded, the Bayesian network model can help determine whether allocating resources to remove the nonnative trout will produce a population with a persistence probability ≥90%, given the current and future temperature regime and stochastic risks. If not, a third alternative is to discontinue active management of CRCT in the fragment, select another fragment that the model indicates does have suitable habitat for the future, and translocate native trout after any nonnatives are removed.

Considering which isolated populations to prioritize in any set under consideration for management (i.e., a portfolio) depends on additional factors not considered in this analysis (Fausch et al. 2009). First, in addition to fragment length, persistence of Westslope Cutthroat Trout increased in fragments with higher habitat quality (Peterson et al. 2014), so habitat protection and restoration are also important goals. Second, resilience of the entire portfolio of CRCT populations to climate change, invasions, and new unknown stressors is likely to be enhanced by sustaining the full range of genetic, morphological, and behavioral diversity, as well as habitat diversity, among the set of populations, just as for other salmonid populations (Schindler et al. 2010; Haak and Williams 2012). In particular, because populations near the periphery of the range can harbor important genetic diversity that allows adaptation to novel future ecosystems, these should be targeted for conservation (Scudder 1989; Haak et al. 2010). Maintaining multiple populations that include the full range of available life history and genetic diversity in a widely distributed mix of large strongholds and smaller fragments will provide the redundancy, representation, and resilience needed to buffer lineages like CRCT against an increasing frequency of natural and human disturbances (Williams et al. 2007; Haak and Williams 2012). The analysis we report here, combining the effects of nonnative trout invaders with a changing climate, is an important step in developing this type of contemporary rangewide strategy for conservation of native Cutthroat Trout in the southern Rocky Mountains.

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