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# Fragmentation and thermal risks from climate change interact to affect persistence of native trout in the Colorado River basin

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## Abstract

Impending changes in climate will interact with other stressors to threaten aquatic ecosystems and their biota. Native Colorado River cutthroat trout (CRCT; *Oncorhynchus clarkii pleuriticus*) are now relegated to 309 isolated high-elevation (>1700 m) headwater stream fragments in the Upper Colorado River Basin, owing to past nonnative trout invasions and habitat loss. Predicted changes in climate (i.e., temperature and precipitation) and resulting changes in stochastic physical disturbances (i.e., wildfire, debris flow, and channel drying and freezing) could further threaten the remaining CRCT populations. We developed an empirical model to predict stream temperatures at the fragment scale from downscaled climate projections along with geomorphic and landscape variables. We coupled these spatially explicit predictions of stream temperature with a Bayesian Network (BN) model that integrates stochastic risks from fragmentation to project persistence of CRCT populations across the upper Colorado River basin to 2040 and 2080. Overall, none of the populations are at risk from acute mortality resulting from high temperatures during the warmest summer period. In contrast, only 37% of populations have a $\geq 90\%$ chance of persistence for 70 years (similar to the typical benchmark for conservation), primarily owing to fragmentation. Populations in short stream fragments <7 km long, and those at the lowest elevations, are at the highest risk of extirpation. Therefore, interactions of stochastic disturbances with fragmentation are projected to be greater threats than warming for CRCT populations. The reason for this paradox is that past nonnative trout invasions and habitat loss have restricted most CRCT populations to high-elevation stream fragments that are buffered from the potential consequences of warming, but at risk of extirpation from stochastic events. The greatest conservation need is for management to increase fragment lengths to forestall these risks.

*Keywords:* climate change, cutthroat trout, fragmentation, multiple stressors, native fish, stream temperature model, stream warming

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## Introduction

The changing climate worldwide has already influenced the distribution and persistence of biota, and this change is predicted to continue (Parmesan & Yohe, 2003; Root *et al*., 2003; Rosenzweig *et al*., 2008). Biota in aquatic ecosystems have been particularly vulnerable, because fishes and aquatic invertebrates are ectothermic and have species-specific temperature requirements that make them sensitive to changes in thermal regimes (Ficke *et al*., 2007; Pörtner & Farrell, 2008). For example, substantial changes in temperatures owing to climate change have been reported for rivers and streams (Webb & Nobilis, 2007; Isaak *et al*., 2012a), and changes to these and other abiotic characteristics have already had strong consequences for many aquatic biota (Burgmer *et al*., 2007; Daufresne & Boet, 2007; Buisson & Grenouillet, 2009). Moreover, fish often will be unable to avoid rising temperatures because their movements are restricted to river networks.

Although temperature is a critical factor affecting aquatic biota in lotic ecosystems, other abiotic variables also alter habitat and shape life histories. Modeling and long-term measurements from western North America have revealed changes in precipitation patterns (Pagano & Garen, 2005) and, more importantly for fishes, the timing and magnitude of stream flows (Luce & Holden, 2009; Clow, 2010; Leppi *et al*., 2012). The

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changing climate is also expected to shift regimes of landscape-level stochastic disturbances like wildfire (Westerling *et al.*, 2006), which could alter stream habitat by increasing the prevalence of postfire landslides (i.e., debris flows) that can inundate streams with sediment (Cannon *et al.*, 2010). Therefore, it is important to include multiple factors and their interactions when addressing how a changing climate could influence populations of aquatic biota such as fishes (Isaak *et al.*, 2012b).

One ecologically and economically important group of fishes that is particularly susceptible to climate change is the salmonids (salmon, trout, and whitefish), a group of stenothermal fishes that require cold water (Jonsson & Jonsson, 2009; McCullough *et al.*, 2009; Isaak *et al.*, 2012b). Research worldwide indicates that increases in stream temperature will influence the distribution and persistence of many salmonid populations (Keleher & Rahel, 1996; Nakano *et al.*, 1996; Hari *et al.*, 2006). For example, recent work from western US mountain systems has predicted that rising water temperatures will truncate stream habitat drastically for all trout species (Rieman *et al.*, 2007; Isaak *et al.*, 2010; Wenger *et al.*, 2011). However, projecting the effects of these changes in climate has been hampered by the coarse resolution of General Circulation Models (GCM). Fortunately, recently developed downscaled climate projections (e.g., Tabor & Williams, 2010; Hostetler *et al.*, 2011) allow increased resolution to match the finer scales at which predictions about aquatic habitat are needed.

For native salmonids, loss of habitat from changes to temperature and flow often combine with invasions by nonnative species to further restrict the native species to fragments of their former habitat (Fausch *et al.*, 2009, 2010; Wenger *et al.*, 2011). Recent research shows that persistence of native species in these isolated habitats is sensitive to fragment size (Rieman & McIntyre, 1995; Morita & Yamamoto, 2002), which influences both the size and genetic integrity of a population (Hilderbrand & Kershner, 2000; Dunham *et al.*, 2004; Young *et al.*, 2005; Neville *et al.*, 2009). Fragment size also influences the risk of extirpation from climate-driven stochastic events such as wildfire and debris flows (Rieman & McIntyre, 1995; Dunham *et al.*, 2003), channel freezing (Chisholm *et al.*, 1987; Lindstrom & Hubert, 2004; Brown *et al.*, 2011), and channel dewatering or drying (Schindler *et al.*, 1996; Jenkins & Keeley, 2010; Leppi *et al.*, 2012).

These climate change–related threats could be particularly troublesome for cutthroat trout (*Oncorhynchus clarkii* spp.), a group of 14 salmonid subspecies native to the western US. Most are restricted to only <1–25% of their historical ranges (Young & Harig, 2001; Behnke, 2002), primarily owing to nonnative trout invasions and habitat loss from various land uses. This fragmentation presumably places many subspecies at risk from climate change (Williams *et al.*, 2009). Colorado River cutthroat trout (CRCT; *Oncorhynchus clarkii pleuriticus*), for example, are currently found in only 14% of their historical range in the upper Colorado River basin, confined to headwater stream fragments above 1700 m in elevation (Hirsch *et al.*, 2006; Young, 2008). Average summer air temperatures in this region of the Southern Rocky Mountains are predicted to increase ~2.7 °C by 2050 (Ray *et al.*, 2008), which can serve as proxy for trends in stream temperatures because both are driven by short- and long-wave solar radiation (Webb *et al.*, 2008). Similar processes are also driving, in part, the earlier snow melt and peak stream discharge that already have been detected for high-elevation streams in Colorado (Clow, 2010; Isaak *et al.*, 2012b). Therefore, to conserve imperiled subspecies like CRCT in the face of climate change, we will need to move beyond predicting shifts in range-wide fish distributions across large areas based solely on temperature and use a more focused approach that addresses multiple interacting threats for specific regions like the upper Colorado River basin.

Here, we develop a Bayesian Network (BN) model to assess how changes in stream temperature interact with stream fragment length to influence the persistence of individual CRCT populations over short-term and long-term time horizons (to 2040 and 2080). To project water temperatures at the scale of stream reaches (~0.1–20.0 km in length), we developed a regional stream temperature model that combines the effects of air temperature changes with landscape characteristics and changes in stream flow to predict CRCT thermal habitat. In turn, changes in air temperature and stream flow are predicted from state-of-the-art dynamical-downscaled regional climate models (Hostetler *et al.*, 2011). We integrate these effects using the BN to create spatially explicit predictions of relative persistence probability for each CRCT population. These results will be useful to help direct management decisions and prioritize restoration activities for imperiled CRCT populations in the face of a changing climate.

## Materials and methods

### *Study area and fish distribution data*

Our study area was the upper Colorado River basin, which includes the Colorado River and all tributaries above Glen Canyon Dam and Lake Powell (Fig. 1a). The upper Colorado River basin lies within the southern Rocky Mountain region of North America which includes several aquatic ecotypes ranging from high alpine streams and lakes to arid lowland rivers.

We restricted our analysis to 309 discrete headwater stream segments (i.e., fragments) known to contain conservation populations of CRCT. Conservation populations are defined as being isolated from nonnative trout, almost always by barriers, and are also free from disease and hybridization with other species (Hirsch *et al.*, 2006). Median length of fragments is only 5.9 km (Fig. 1b), owing to this isolation. Each CRCT segment is composed of multiple National Hydrography Dataset Plus (NHDPlus; 1 : 100 000; http://www.horizon-systems.com/nhdplus) stream reaches. All study streams are ≥1700 m in elevation, and found primarily on public lands in three states (CO, UT, WY). Locations, downstream barriers, upstream extent of stream use by CRCT, and status of CRCT conservation populations were determined from the most recent CRCT Conservation Team range-wide database (2009), first described in Hirsch *et al.* (2006).

### *Bayesian network model*

We developed a BN model to predict the effects of lotic thermal conditions and stream fragment length on the relative persistence of CRCT populations for 30 and 70 years after 2010 (i.e., 2040 and 2080). The graphically based modeling framework of BNs is flexible and easily interpreted (Marcot *et al.*, 2006), and their use is increasing in ecology and conservation biology (Rieman *et al.*, 2001; Peterson *et al.*, 2008; Stewart-Koster *et al.*, 2010). Two key steps in creating a BN are: (i) constructing a directed acyclical graph (DAG) that depicts important interactions among variables (nodes) that influence model outcomes (here, CRCT persistence), and (ii) defining states within each node. In our case, temperature regimes affect CRCT survival, growth, and reproduction (Fig. 2). Likewise, stream fragment length determines population genetic factors and the ability to buffer against stochastic factors, which together affect the habitat capacity of the segments. In turn, habitat capacity interacts with temperature to affect persistence of CRCT populations.

We sought to create a relatively simple BN that included the essential processes that govern CRCT persistence in stream fragments, so that it will be readily understood and used by a variety of practitioners (e.g., research scientists and resource managers). We used established objective methods to develop the BN (Marcot *et al.*, 2006; Marcot, 2012), and sought independent review from outside users and experts at two stages. First, the first three coauthors collaborated to develop the initial DAG, creating the structure whereby parent nodes (e.g., stream temperature and fragment length) feed information to child nodes (e.g., effective population size, habitat capacity/potential). Second, these authors developed narratives and defined states for each node using a combination of data from refereed literature and expert opinion. Third, we sought initial peer review of the DAG, narratives, and node states from four outside users, all state and federal fishery biologists who manage CRCT conservation populations. Fourth, after revising the BN based on these reviews, the three coauthors each independently defined the conditional probabilities at every child node for each combination of parent node states, the final step in developing the BN. Fifth, after reconciling minor differences in the conditional probabilities, we completed final calculations of CRCT population persistence and prepared the manuscript. We then sought a second independent peer review from two research scientists who are

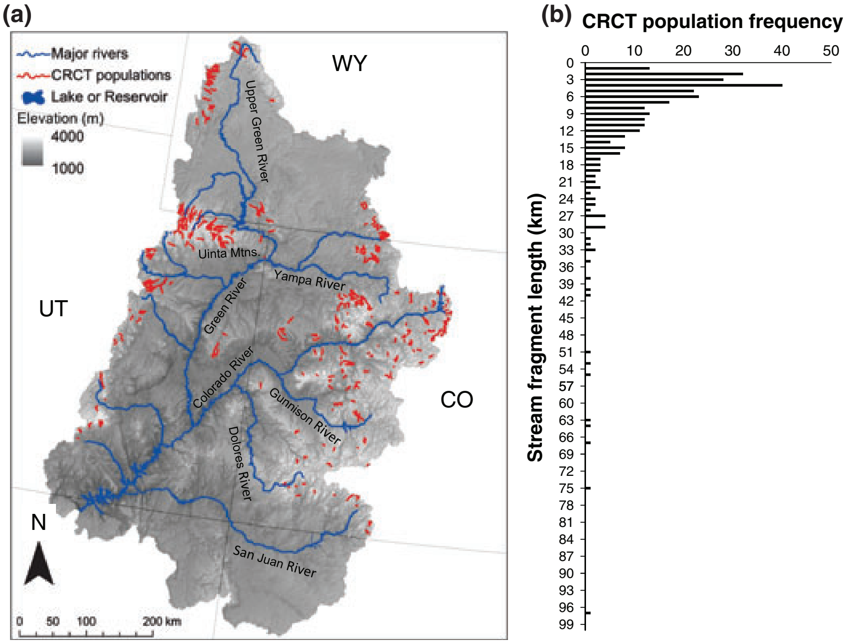

**Fig. 1** Location, elevation, and fragment length of the Colorado River cutthroat trout (CRCT) conservation populations. Panel (a) shows the location of the CRCT populations, and the major rivers and states in the upper Colorado River basin. Panel (b) shows the length (km) frequency distribution of stream fragments for all 309 CRCT conservation populations (median length = 5.9 km).

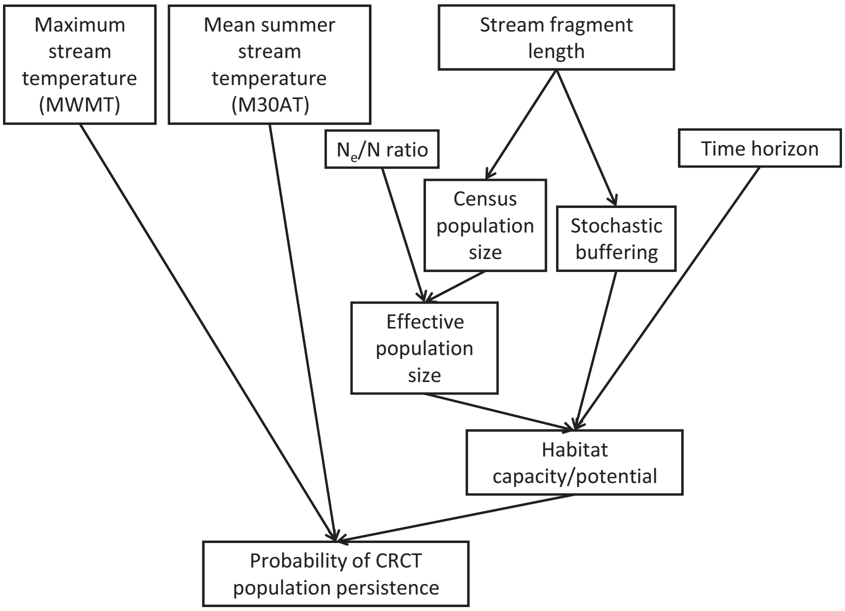

**Fig. 2** The directed acyclical graph used to structure the Bayesian network (BN) model, which predicts the future persistence of Colorado River cutthroat trout (CRCT) populations.

experts in cutthroat trout ecology and conservation, and have modeled climate change and used BNs for stream salmonids. Finally, we assessed the validity and behavior of our BN using established protocols (Marcot *et al.*, 2006; Marcot, 2012), including testing the sensitivity of our predictions of CRCT population persistence to each node (see S-Bayesian Network sensitivity).

### *Node and state definitions*

*Temperature requirements for survival.* Maximum stream temperature is often assumed to be a strong determinant of species distributions where populations are close to the upper thermal tolerance limit of a species. To represent this, we calculated the Maximum Weekly Maximum Temperature (MWMT), which is the average of the daily maximum temperatures for the warmest 7-day period. This metric represents the extreme peaks that cause trout mortality, which we used to define the upper limit of thermal habitat suitable for persistence of CRCT populations. However, this thermal threshold for survival is more liberal than existing criteria used to define upper thermal conditions that are safe for cutthroat trout and prevent any deleterious effects (e.g., Todd *et al.*, 2008).

Investigators conducting field and laboratory studies of lethal temperatures for cutthroat trout have measured three different criteria: Upper Incipient Lethal Temperatures (UILT), Ultimate Upper Incipient Lethal Temperature, and Critical Thermal Maxima (CTM) values (Johnstone & Rahel, 2003; Bear *et al.*, 2007; Underwood *et al.*, 2012; S-Bayesian Network node and state definitions). Criteria for two cutthroat trout subspecies are most relevant for our purpose. The 7-day UILT for Bonneville cutthroat trout (*Oncorhynchus clarkii utah*), a neighboring and evolutionarily similar subspecies to CRCT (Behnke, 2002; Loxterman & Keeley, 2012), is 24.2 °C (Johnstone & Rahel, 2003) and the CTM is 29.7 °C (Wagner *et al.*, 2001). The CTM for CRCT acclimated at 20.0 °C is 29.4 °C (Underwood *et al.*, 2012). Therefore, we reasoned that the lethal MWMT for CRCT is between 24.2 and 29.4 °C (S-Bayesian Network node and state definitions).

Diel temperature fluctuations in streams can allow fishes to survive above the lethal limits measured at constant temperatures in the laboratory. Johnstone & Rahel (2003) measured the upper lethal limit for Bonneville cutthroat trout under diel fluctuations of 10–13 °C reported from the field (Schrank *et al.*, 2003) and found they survived until maximum temperatures reached 28 °C. Temperature records from CRCT streams $\geq 1700$ m elevation ($n = 146$) for the warmest 7 days of the year that make up the MWMT showed that the diel range averaged 7.4 °C, similar to that used by Johnstone & Rahel (2003). Also, the mean daily maximum of the 7 days comprising the MWMT for CRCT streams had a standard deviation of 1.1 °C. Therefore, we reasoned that a MWMT of 26.0 °C would be within ~2 SD of the maximum daily temperature of 28.0 °C that likely causes death under diel fluctuations like those in natural streams, and selected a MWMT $\geq 26.0$ °C as the upper limit for CRCT population persistence (Table 1; S-Bayesian Network node and state definitions).

*Temperature requirements for growth and recruitment.* The temperature metric most relevant for growth and recruitment of CRCT is the maximum 30-day average temperature (M30AT), determined annually, which measures the mean temperature for approximately the warmest month. Two laboratory experiments investigating the effects of constant temperature on growth of cutthroat trout, using constant or maximum rations, showed that growth reached 75–100% of

**Table 1** Bayesian network node descriptions and the corresponding states for each node. Input data (I) are shown for the five input parent nodes

| Node name | Definition | States |
|---|---|---|
| Maximum stream temperature (MWMT; I) | The warmest 7-day mean of the maximum daily stream temperature, used to evaluate survival | Survival: <26.0 °C<br>Mortality: $\geq$26.0 °C |
| Mean summer stream temperature (M30AT; I) | The warmest 30-day mean of the average daily stream temperature, used to evaluate recruitment and growth | No recruitment: <8.0 °C<br>Low recruitment: 8.0–9.0 °C<br>Optimal growth and recruitment: 9.1–18.0 °C<br>Declining growth: 18.1–19.9 °C<br>Low or no growth: $\geq$20.0 °C |
| Stream fragment length (I) | Stream length for individual CRCT segments indentified in the Colorado River Cutthroat Trout Conservation Team range-wide database | 0.02–96.4 km |
| Time horizon (I) | Time period for predicting population persistence | Short: 30 years (2040)<br>Long: 70 years (2080) |
| $N_e/N$ ratio (I) | Proportion of census population ($N$) contributing unique genetic diversity to the population | 0–1 (0.25)* |
| Effective population size | Effective population size ($N_e$; shown in parenthesis) estimated from the $N_e/N$ ratio, based on the estimate of $N$ predicted from stream fragment length (Young *et al.*, 2005) | *Potential genetic consequences*<br>Immediate negative: ($N_e$ < 50) <1.7 km<br>Short-term negative: ($N_e$ = 51–200) 1.7–4.6 km<br>Long-term negative: ($N_e$ = 201–500) 4.7–7.7 km<br>Robust: ($N_e$ > 500) >7.7 km |
| Stochastic buffering | The capacity of the stream fragment to buffer the CRCT population against fire, debris flow, freezing, and drying | Limited buffering: <3.6 km<br>Variable buffering: 3.6–7.2 km<br>Robust buffering: >7.2 km |
| Habitat capacity/potential | The capacity for the stream segment to maintain a viable CRCT population, based on combined influences of $N_e$ and stochastic buffering | Low<br>Moderate<br>High |
| Probability of CRCT population persistence | The probability of persistence (>20 adult fish total) for an individual CRCT population over the time horizon | Persist<br>Extirpated |

*$N_e/N$ ratio synthesized from literature for salmonids and used in all our model runs. However, our BN structure allows for input of any proportional value from 0 to 1.

the maximum rate between 9.5 and 18.0 °C (Bear *et al.*, 2007; Brandt, 2009). These studies also showed that growth declined markedly below 9.0 °C and above 18.0 °C, and was only 25–50% of optimal growth or less above 20.0 °C (S-Bayesian Network node and state definitions).

Monthly temperature metrics are also a good indicator of recruitment, so M30AT was also used to assess recruitment potential for CRCT. This metric is similar to mean July or August temperatures, which were found in previous research to indicate suitable thermal conditions for recruitment of two neighboring subspecies of cutthroat trout (greenback cutthroat trout *Oncorhynchus clarkii stomias*; Rio Grande cutthroat trout *Oncorhynchus clarkii virginalis*; Harig & Fausch, 2002). Field studies (Harig & Fausch, 2002; Coleman & Fausch, 2007a) and laboratory experiments (Coleman & Fausch, 2007b) indicated that a minimum thermal threshold of 8.0 °C M30AT is needed to support minimal CRCT recruitment and $\geq$9.0 °C is required for consistently high recruitment. To describe the effect of stream temperature on CRCT recruitment and growth, we integrated the above information to create five nodes states (no recruitment, low recruitment, optimal growth, declining growth, and low or no growth; Table 1; S-Bayesian Network node and state definitions).

### *Stream fragment length*

*Effective population size.* To ensure the persistence of a population, individuals must display sufficient genetic variation to allow population adaptation given ecological and evolutionary constraints. Allendorf & Luikart (2009) proposed that to ensure long-term population persistence, an effective population size ($N_e$) of at least 500 is required. In general, populations with $N_e$ < 50 are believed to be in danger of immediate deleterious inbreeding effects, whereas those with $N_e$ between 50 and 500 are of intermediate concern (Rieman & Allendorf, 2001). For these intermediate population sizes, we inferred that those between 50 and 200 are at risk of negative genetic consequences over the short term (i.e., <30 years, by 2040) whereas those between 201 and 500 are somewhat buffered from short-term effects, but at risk over the long term (i.e., 70 years, by 2080).

The effective population size is generally smaller than the total or census population ($N$). Effective population size represents the size of an ideal population (i.e., with discrete cohorts, equal sex ratio, random mating, constant size, and equal reproduction probability; Frankham, 1995) that would experience the same amount of genetic drift as the actual population of interest (Wright, 1969). One common way to infer $N_e$ from $N$ is to apply a $N_e/N$ ratio. Values of $N_e/N$ ratios reported for stream-resident salmonids range from 0.15 to 0.50 (Rieman & Allendorf, 2001; Palm *et al.*, 2003; Jensen *et al.*, 2005). Therefore, we used a $N_e/N$ ratio of 0.25 to estimate $N_e$, which is in the lower half of the range reported and should result in conservative estimates. This value is also similar to the $N_e/N$ ratio of 0.20 used previously to assess the persistence of cutthroat trout populations (Hilderbrand & Kershner, 2000).

Young *et al.* (2005) developed a relationship predicting census population size from fragment length for CRCT and greenback cutthroat trout in 31 streams. Their data were best described by a positive linear relationship between stream fragment length (km) and the square root of cutthroat trout abundance. We combined this with our $N_e/N$ ratio to determine the minimum CRCT segment length required to meet our four $N_e$ criteria (Table 1). This created four states of risk for genetic consequences, ranging from populations at immediate risk (<1.7 km = $N_e < 50$ CRCT), to those with genetic variability sufficient to allow adaptation to potential evolutionary and environmental constraints for at least 70 years (>7.7 km = $N_e > 500$ CRCT; see S-Bayesian Network node and state definitions).

*Stochastic environmental factors*. Stream fragment length also affects the persistence of cutthroat trout populations by influencing the incidence of internal refuges from stochastic disturbance, such as wildfire (Rieman & Clayton, 1997; Brown *et al.*, 2001; Dunham *et al.*, 2007), debris flows (Gresswell, 1999; Cannon *et al.*, 2010), and stream drying and freezing (Hubert *et al.*, 2000; Lindstrom & Hubert, 2004). A summary of the available information revealed similar thresholds for stream fragment length at which populations are highly susceptible to stochastic risks (<3.6 km), vs. those that are at variable risk (3.6–7.2 km), or robust to these risks (>7.2 km; Table 1). For example, bounded alluvial valley segments (BAVS) are geomorphic features that create low-gradient meadow segments with sufficient groundwater to prevent freezing and drying within Rocky Mountain stream networks, and tend to occur at relatively regular intervals of about 3.6 km (Baxter *et al.*, 1999; Baxter & Hauer, 2000). Likewise, other studies indicate that native trout in stream fragments shorter than about 3 km are at high risk of extirpation from wildfire, whereas those in stream fragments longer than about 6 km are at low risk because of spatial heterogeneity in burns and internal refuges for fish (Rieman & Clayton, 1997; Brown *et al.*, 2001). After fire, habitat in headwater stream fragments is at risk of inundation by colluvial debris flows, with those <7.2 km long most susceptible (Cannon *et al.*, 2010; S-Bayesian Network node and state definitions-Debris flows; Figure S1). We combined all these stochastic risks into one set of nodes states because the thresholds for stream fragment length are similar, based on the evidence available and our own experience. Overall, we expect that longer stream fragments can better buffer these stochastic factors, because wildfires and debris flows are patchy in space or have limited spatial extent, and because longer stream fragments are likely to have internal refuges from drying and freezing created by alluvial geomorphic features (e.g., BAVS, beaver dams) that supply groundwater (Table 1; S-Bayesian Network node and state definitions).

### *Bayesian network input variables*

Our goal was to predict the relative probability of persistence for each of the 309 CRCT conservation populations in the upper Colorado River basin under present conditions, and under altered conditions of air temperature and flow regimes 30 and 70 years in the future (2040 and 2080). We used a Geographic Information System (GIS) to measure the length of stream fragments with conservation populations (termed CRCT segments, hereafter), which we assumed would not change through time. The downstream ends of nearly all CRCT segments are set by barriers like water diversions, culverts, or natural waterfalls that prevent upstream invasion by nonnative trout. We then developed a stream temperature model to predict the two temperature metrics (MWMT and M30AT) for each CRCT segment, based on future air temperature and flow predicted by dynamically downscaled climate models. Here, we describe the data and statistical techniques we used to create the stream temperature model, and the climate models used to provide the inputs.

### *Stream temperature model*

To predict the two stream temperature metrics (MWMT and M30AT) for the 309 CRCT segments, we developed and compared stream temperature models for each metric using three different statistical methods. Our models predict stream temperature from three types of covariates: air temperature, summer stream flow, and a set of landscape and geomorphic variables. Each CRCT segment was made up of multiple smaller stream reaches, defined by discrete NHDPlus reaches. Stream temperatures were predicted for each stream reach and then averaged for the CRCT segment, to estimate the mean thermal conditions for each CRCT population. We used this approach to dampen the effects of unsuitably warm or cold reaches, and assumed that fish could find refuge in other suitable reaches when they are available within a given stream fragment.

*Stream temperatures.* Stream temperature records were gathered from online US Geological Survey (USGS) records, state and federal agencies, and university researchers. These records were variable in duration and timing, so we used specific criteria to select a subset that fit our needs. We included only records from known geographical locations (with X and Y coordinates) that encompassed at least one full summer season (June–September). We treated each year as an independent observation point, but limited the data from each site to 3 years. When sites had longer records, we used the maximum, minimum, and middle (closest to the mean) years for MWMT and M30AT to avoid biasing results by using more than 3 years of observations from one site, and to help achieve spatial balance across our sampling locations.

We obtained stream temperature records for 363 sites and we were able to use 274 of them for our stream temperature model, resulting in 482 observation points of summer stream temperature. The temporal resolution for all records ranged between 15 and 60 min. We found few stream temperature records from the Upper Green River and Uinta Mountains in the northwest part of the basin, and from southern areas of the basin. Therefore, to increase the spatial distribution of stream temperature data, we also used records from 15 sites nearby in the Great Basin (Thomas and Smith's Forks of the Bear River) to the northwest, and 18 in the Rio Grande River basin to the southeast.

*Model covariates.* We used ArcGIS 9 (ArcMap 9.3.1; ESRI Redlands, CA, USA) and extracted attributes for each thermograph site from multiple databases. Covariates were chosen based on previous regional stream temperature models (Wehrly *et al.*, 2009; Isaak *et al.*, 2010) and mechanistic studies of stream thermal budgets (Webb *et al.*, 2008). This previous research indicated that ambient temperature, geomorphology, and landscape position are important drivers and predictors of stream temperature. We selected 11 covariates, of which two measured air temperature, two measured summer stream flow, three indicated landscape position, and four represented geomorphic characteristics (Table 2).

To estimate air temperature for high-elevation areas throughout the upper Colorado River basin, we created a database of all the SNOTEL sites (http://www.wcc.nrcs.usda.gov/snow/) within the basin in Colorado, Wyoming, and Utah that had continuous daily air temperature data from 1986 to 2010. We then determined the closest (via Euclidian distance) SNOTEL site from each thermograph site and used it to estimate the air temperature covariates for that thermograph site. Air temperatures were summarized using the same short-term (MWMT) and long-term (M30AT) summer thermal metrics used for water temperature. We obtained records for 34 sites in the SNOTEL network that fit our criteria for use in stream temperature models.

We also gathered data for stream flow, for use as a regional indicator of the relative magnitude of annual summer flow which also influences water temperature. First, we used a nation-wide database of USGS stream flow gages (http://waterdata.usgs.gov), and selected those that are minimally affected by water diversions and dams (Falcone *et al.*, 2010). We summarized summer flows (June–August) by calculating two metrics, summarized annually: (i) the overall mean daily discharge (Q_sumr), and (ii) the relative summer flow (i.e., the mean flow for a given summer divided by the long-term mean for that site; Q%_sumr) for the period of record at each gage. We selected 54 gage sites that fit our criteria. Lastly, we determined the closest (Euclidian distance) gage with an overlapping temporal range for each thermograph site, and used data from it to calculate the flow covariates for that thermograph.

For each thermograph site, latitude (Latitude) was determined using GPS coordinates; point elevation (Elv_pt) was estimated using a 30 m resolution digital elevation model from the National Elevation Dataset (NED; http://ned.usgs.gov/) and GIS tools; and elevation of the stream reach (Elv_rch) was estimated from the NHDPlus dataset which

**Table 2** Model selection results for the multiple regression models to predict the two stream temperature metrics, based on the Akaike information criterion (AIC$_c$). The AIC$_c$ scores for the best model for each temperature metric are shown in **bold** and underlined. See text for definitions of variables

| | | | | | | | | AIC$_c$ | |
|---|---|---|---|---|---|---|---|---|---|
| Model | Covariates | | | | | | | MWMT | M30AT |
| 1 | Air temp. | Latitude | Drng_area[*] | Slope | Aspect | Elv_rch[‡] | Q_sumr[¶] | **2374.63** | 2110.90 |
| 2 | Air temp. | Latitude | Drng_area | Slope | Aspect | Elv_rch | Q%_sumr[‖] | 2380.67 | **2109.42** |
| 3 | Air temp. | Latitude | Drng_area | Slope | Aspect | Elv_pt[§] | Q_sumr | 2384.18 | 2117.45 |
| 4 | Air temp. | Latitude | Drng_area | Slope | Aspect | Elv_pt | Q%_sumr | 2389.78 | 2115.44 |
| 5 | Air temp. | Latitude | Twi$^{+}$ [†] | | | Elv_rch | Q_sumr | 2395.94 | 2118.94 |
| 6 | Air temp. | Latitude | Twi$^{+}$ | | | Elv_rch | Q%_sumr | 2402.07 | 2118.10 |
| 7 | Air temp. | Latitude | Twi$^{+}$ | | | Elv_pt | Q_sumr | 2408.10 | 2136.60 |
| 8 | Air temp. | Latitude | Twi$^{+}$ | | | Elv_pt | Q%_sumr | 2413.85 | 2135.36 |

*Cumulative upstream drainage area.

†Topographic wetness index plus (Theobald, 2007).

‡Average elevation for an entire stream reach.

§Elevation at the thermograph point.

¶Average summer (June–September) stream discharge.

‖Summer (June–September) discharge as a percentage of annual average discharge.

reports the average elevation for each stream reach. Four geomorphic characteristics were measured for each thermograph site: slope, cumulative drainage area [Drng_area], aspect (estimated at the point location of the thermograph), and Topographic Wetness Index+ [TWI$^+$; a measure of potential for overland flow based on solar insolation, hillslope, and aspect]. We used the NHDPlus stream network data layer to determine the slope (estimated from values within each stream reach) and cumulative drainage area for the NHDPlus stream reach in which each thermograph site was located. We used 30 m resolution NED and GIS tools to determine aspect and TWI$^+$ (LCaP v1.0; Theobald, 2007) for each thermograph site.

*Model development.* We used three different statistical modeling techniques to explore the ability of the covariates to predict stream temperatures. These three approaches varied in complexity, and were evaluated using cross-validation procedures. We performed separate analyses for MWMT and M30AT to determine the best approach for predicting each stream temperature metric.

The simplest modeling technique was multiple linear regression (LR). Eight subsets of covariates were used when fitting this model to avoid colinearity among several correlated variables (e.g., elevation of the segment vs. elevation of the point; Table 2). We used model selection based on an information-theory criterion (Burnham & Anderson, 2002) to select the top model (i.e., the subset of covariates with the lowest Akaike information criterion, corrected for small sample size; AIC$_c$) for each stream temperature metric. We evaluated the same set of eight predictive candidate models for both stream temperature metrics.

Second, to account for potential spatial autocorrelation of lotic thermal conditions, we used universal kriging (UK; Stein & Corsten, 1991). The advantage of using UK is the ability to integrate the predictive power of covariates in a linear fashion while also incorporating the spatial autocorrelation of the residuals, to gain additional predictive power using geostatistical methods. We used the covariates from the top model identified in our LR analysis (above) along with the $X$ and $Y$ coordinates of each site to create variograms and determine the best fit given the spatial structure of the residuals.

Finally, we also fit models using the machine-learning regression tree technique termed Random Forests (RF; Cutler *et al.*, 2007). We used the entire set of covariates for this approach, because the method produces and then combines a suite of different models based on the covariates. Using RF maximized our predictive potential, but sacrificed some ability to interpret individual covariates. An advantage of RF over LR and UK is that no assumptions are made about the distribution of data or the nature of relationships between predictor and response variables (Cutler *et al.*, 2007). We used standard option settings for our RF, which included a maximum of 500 trees and selecting from three variables at each split.

To select the best predictive model for each stream temperature metric based on our three statistical techniques, we used a ten-fold cross-validation technique, with unique subsets. We compared the average root mean square prediction error (RMSPE; Power, 1993) across all ten-folds as a measure of model fit for the three statistical techniques. For each metric, the model with the lowest RMSPE was used to predict stream temperature metrics in subsequent analyses.

*Climate projections.* To represent future climate conditions (i.e., air temperature and stream flow), we used dynamically downscaled output from a regional climate model (RegCM3; Hostetler *et al.*, 2011). Compared to statistical downscaling, dynamical downscaling depicts climate processes more accurately in areas of complex terrain. In brief, RegCM3 produces high resolution climate projections (15 × 15 km grid cells) using a GCM to represent boundary conditions. We used output from RegCM3 for two GCM inputs (MPI ECHAM5 [ECH] and PSU/OSU GENMOM [GNM]; Hostetler *et al.*, 2011) and the A2 emission scenario, which assumes higher emissions and thus serves as a worst case situation (IPCC, 2007). The two GCMs used for these projections have similar sensitivities to increases in CO$_2$ (ECH 2–4 °C; GNM 2–3 °C). Predictions from the ECH model for temperature and precipitation are close to the average of eight commonly used GCMs, whereas predictions from the GNM model are biased toward cooler and wetter projections (Hostetler *et al.*, 2011). Our goal was to examine the influence of the average future climate at two time horizons (2040 and 2080), so we averaged climate model output for each GCM from three periods: 2005–2010 (current scenario; no projections were available for 2000–2004), 2035–2045 (short-term; 2040), and 2075–2085 (long-term; 2080). Although we realize that fish populations also may be strongly affected by extreme climate events (e.g., drought and heat waves; IPCC, 2007; Meehl *et al.*, 2009), unfortunately current climate models are unable to predict these events with sufficient accuracy to be useful for analyses like ours (Coumou & Rahmstorf, 2012).

We used these dynamically downscaled climate projections for surface air temperature and total runoff as inputs to the stream temperature model to predict M30AT and MWMT under future conditions. We used the predicted surface air temperature from the grid cell within which each SNOTEL site was located. We used the model output for total runoff and ArcGIS 9.3 hydrology tools to estimate changes in stream flow for each gage site. To avoid model bias (i.e., consistent differences between model output and observed values), we determined the percentage change in modeled air temperature and total runoff from the average current values to the averages for the short- and long-term future periods, for each climate model. We then calculated the future values by multiplying the current (2000–2009) observed values (i.e., those from the SNOTEL and flow gage databases) by these percentages, and used these in our stream temperature model to make predictions of future water temperature.

## *Predictions of CRCT population persistence*

We predicted the two water temperature metrics for each of the NHDPlus reaches that make up each CRCT segment using the best model of stream temperature for each metric, along with the covariates and climate projections described previously. The midpoint of each NHDPlus stream reach was used to determine the closest SNOTEL site and gage station from which the predicted air temperature and stream flow values where gathered. Stream temperature predictions for each NHDPlus reach were then averaged for each CRCT segment, and these were used with the CRCT segment length as input to the BN model to predict the relative probability of persistence for each CRCT population. To examine regional trends for these CRCT populations, we summarized model outputs for the eight major river basins (i.e., 4-digit USGS Hydrologic Unit Codes). All BN development and analyses were performed using Netica software 4.16 (Norsys Software Corp., Vancouver, BC, Canada). All stream temperature model fitting and prediction analyses were performed using the statistical package R 2.14.2 (R Development Core Team, 2012) with the following libraries: geoR (Ribeiro & Diggle, 2001) and randomForest (Liaw & Wiener, 2002).

## Results

### *Stream temperature model*

*Model selection.* We determined that the best subset of covariates (based on $AIC_c$) to predict MWMT and M30AT differed only in the identity of the summer flow covariate (Table 2; Table S5; Fig. S8). Based on the RMSPE, the best model for MWMT was the RF model whereas the best M30AT model was the UK model (Figs S2 and S3). The prediction error (i.e., RMSPE) for the best-supported model was less for M30AT (1.98 °C) than MWMT (2.79 °C), and both of these are similar to the RMSPE reported for other regional stream temperature models (e.g., Wehrly *et al.*, 2009). These three modeling techniques differed most in their ability to accurately predict high stream temperatures (>20 °C M30AT; >25 °C MWMT). At these high temperatures, predictions of M30AT by the UK model were closest to the observed values most often (in 25 of 34 cases where observed values were >20 °C; Fig. S4), and predictions of MWMT by the RF model were closest to the observed values most often (in 16 of 34 cases where values were >25 °C; Fig. S5). However, the best models predict high M30AT values better than high MWMT values, and both models underestimate these high temperatures. As a result, the models will tend to overestimate our predictions of growth, and especially survival, at high temperatures, requiring us to be conservative in our conclusions about CRCT population persistence in segments predicted to have high temperatures.

*Predicted thermal conditions for CRCT populations.* We summarized the predicted thermal conditions for CRCT segments by averaging across the two dynamically downscaled GCMs. Overall, the models predicted little change in either stream temperature metric by 2040, but by 2080 these temperature metrics are predicted to increase 0.3–1.8 °C, on average (Table 3; see S-Stream temperature model covariate assessment for model structure). However, none of the 823 NHDPlus reaches within the 309 CRCT segments are predicted to be lethal to CRCT by 2080 (i.e., MWMT $\geq$ 26.0 °C; Table S1; Fig. S6), and <1% are predicted to have temperatures too warm for growth (i.e., M30AT $\geq$ 20.0 °C), although these results may be conservative (see above). In addition, the model predicts that by 2080 only 128 reaches (16%) will have MWMT $\geq$ 23.0 °C, the approximate temperature where our model begins to underestimate MWMT values (Fig. S5). These results indicate that high temperatures are unlikely to cause widespread outright mortality, or even low growth, by 2080. In contrast, a large percentage (86%) of NHDPlus stream reaches are predicted to have M30AT between 9.1 and 18.0 °C, and thus be optimal for growth and recruitment in 2080 (Table S1; Fig. S6). Variation in M30AT predictions, as indicated by the standard deviation (SD), was greatest in areas with the fewest temperature records (e.g., Uinta Mountains, Upper Green River; Fig. S7).

### *Bayesian network model*

*Model sensitivity and behavior.* The conditional probability tables for the two child nodes with more than one parent input node show how each unique combination of node states influences habitat capacity and probability of CRCT population persistence (Tables S2 and S3). The two types of sensitivity analyses show that predictions of CRCT population persistence are always most sensitive to the predicted values of M30AT (Table S4; Fig. 3). For our application of this BN over the range of variable values found among CRCT populations, predicting CRCT persistence is most sensitive to M30AT and second most sensitive to fragment length, whereas CRCT persistence is least sensitive to time and MWMT (Fig. 3a). When evaluating our BN over the entire range of each input variable, predicting CRCT persistence is again most sensitive to M30AT, and second most sensitive to MWMT (Fig. 3b). These results validate that our BN model captures the intended processes and interactions sufficiently to jointly address the effects of fragment length and changing thermal conditions on CRCT population persistence.

*Predicted persistence of CRCT populations.* The persistence of CRCT populations predicted from the BN model shows almost no change by 2040, but by 2080 there is an overall decrease in population persistence (Table 3). More detailed analysis revealed that CRCT populations in fragments $\geq$7 km long have a high pre-

**Table 3** Mean current and predicted values for stream physical and thermal characteristics, and persistence of Colorado River cutthroat trout (CRCT) populations. Maximum weekly maximum temperature (MWMT; °C) and maximum 30-day average temperature (M30AT; °C) are shown for the 2000s (2000–2009), along with the predicted change in these stream temperature metrics (°C) by 2080 (2075–2085). Values for CRCT population persistence are shown for the current period (2000s; 2000–2009) and through short-term (2040; 2035–2045) and long-term (2080; 2075–2085) time horizons for each major upper Colorado River drainage basin

| River basin* | CRCT populations | Stream length (km) | MWMT 2000s | M30AT 2000s | MWMT change by 2080 | M30AT change by 2080 | CRCT persistence 2000s | CRCT persistence 2040 | CRCT persistence 2080 |
|---|---|---|---|---|---|---|---|---|---|
| Upper Green | 68 | 15.0 | 18.5 | 12.1 | 1.2 | 1.0 | 0.89 | 0.89 | 0.86 |
| Lower Green | 37 | 17.0 | 19.0 | 13.9 | 1.3 | 1.0 | 0.86 | 0.86 | 0.82 |
| Yampa | 58 | 11.7 | 19.9 | 14.3 | 1.1 | 1.1 | 0.81 | 0.81 | 0.78 |
| Upper Colorado | 82 | 7.0 | 16.0 | 11.5 | 1.4 | 1.1 | 0.69 | 0.70 | 0.72 |
| Gunnison | 29 | 5.8 | 16.3 | 12.3 | 1.8 | 1.2 | 0.72 | 0.72 | 0.69 |
| Dolores | 5 | 6.8 | 17.7 | 13.7 | 0.3 | 0.9 | 0.89 | 0.89 | 0.84 |
| San Juan | 12 | 6.3 | 15.9 | 11.5 | 0.7 | 1.0 | 0.77 | 0.77 | 0.75 |
| Lower Colorado | 18 | 4.9 | 18.2 | 14.0 | 0.7 | 1.0 | 0.73 | 0.73 | 0.68 |

*See Fig. 5 for location of basins.

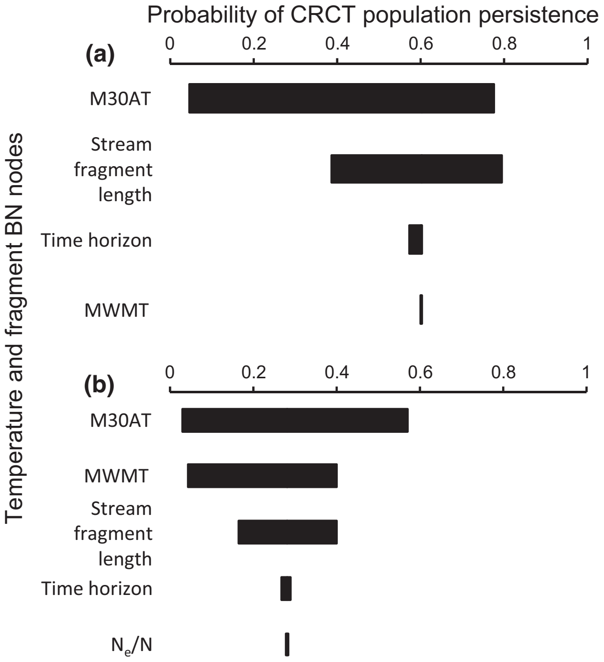

**Fig. 3** Tornado diagrams showing the sensitivity of predicted Colorado River cutthroat trout (CRCT) persistence to each node in the Bayesian network (BN) model. Shown are the sensitivity results for the range of values found in the CRCT database (a) and for the theoretical maximum range of each input variable (b).

dicted probability of persistence to 2080. In contrast, those in short fragments $\leq 4$ km long are predicted to have much lower probability of persistence, and the predicted persistence of those 2–4 km long are most likely to decline significantly by 2080 (Fig. 4). Moreover, warming of some reaches in cold high-elevation CRCT segments around the midlatitudes in the eastern portion of the UPCO basin actually increases the predicted persistence of those populations. In contrast, the CRCT populations in short segments at lower elevations appear to be at the greatest risk of extirpation from climate change–induced factors by 2080, although populations with a predicted persistence <0.50 make up a small proportion for any subbasin (Fig. 5). Even the major river drainages in the southern half of the basin that have few populations (e.g., Dolores, San Juan, and Lower Colorado) were not predicted to lose many entire populations. The Upper Green drainage basin is predicted to have the most robust CRCT populations, likely owing to a combination of longer fragments and higher latitude.

## Discussion

Our results indicate that the current restricted distribution of CRCT populations reduces the potential thermal impacts of climate change, but the high degree of fragmentation increases their susceptibility to catastrophic stochastic events. Although the stream temperature models predict continued warming of headwater habitats in the upper Colorado River basin from the present through 2080, in many locations water temperatures remain well within the range suitable for thriving CRCT populations. For a small number of these CRCT segments conditions are actually predicted to improve because streams are currently too cold for adequate reproduction (Harig & Fausch, 2002; Coleman & Fausch, 2007a). However, the shorter the stream frag-

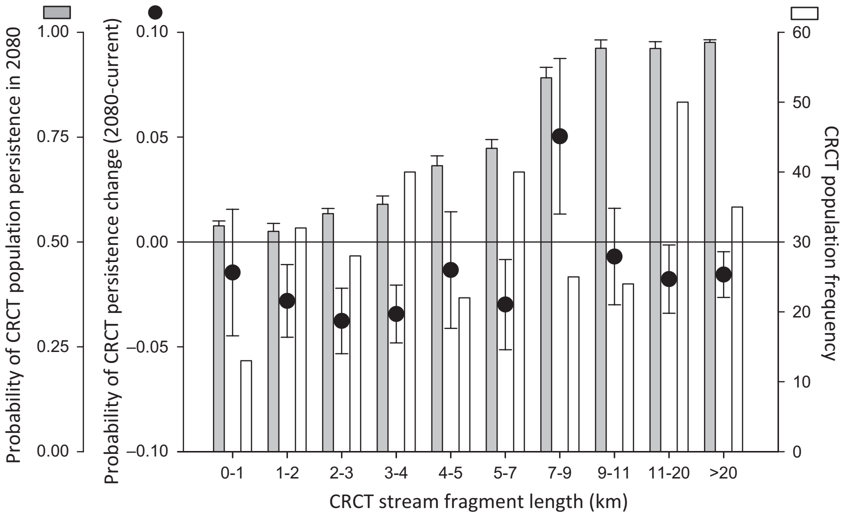

**Fig. 4** The predicted persistence for Colorado River cutthroat trout (CRCT) conservation populations in 2080, and the change in predicted population persistence from the current period to 2080, grouped by CRCT segment length categories. The frequency of populations within each length category is also shown. Error bars represent ±1 SE.

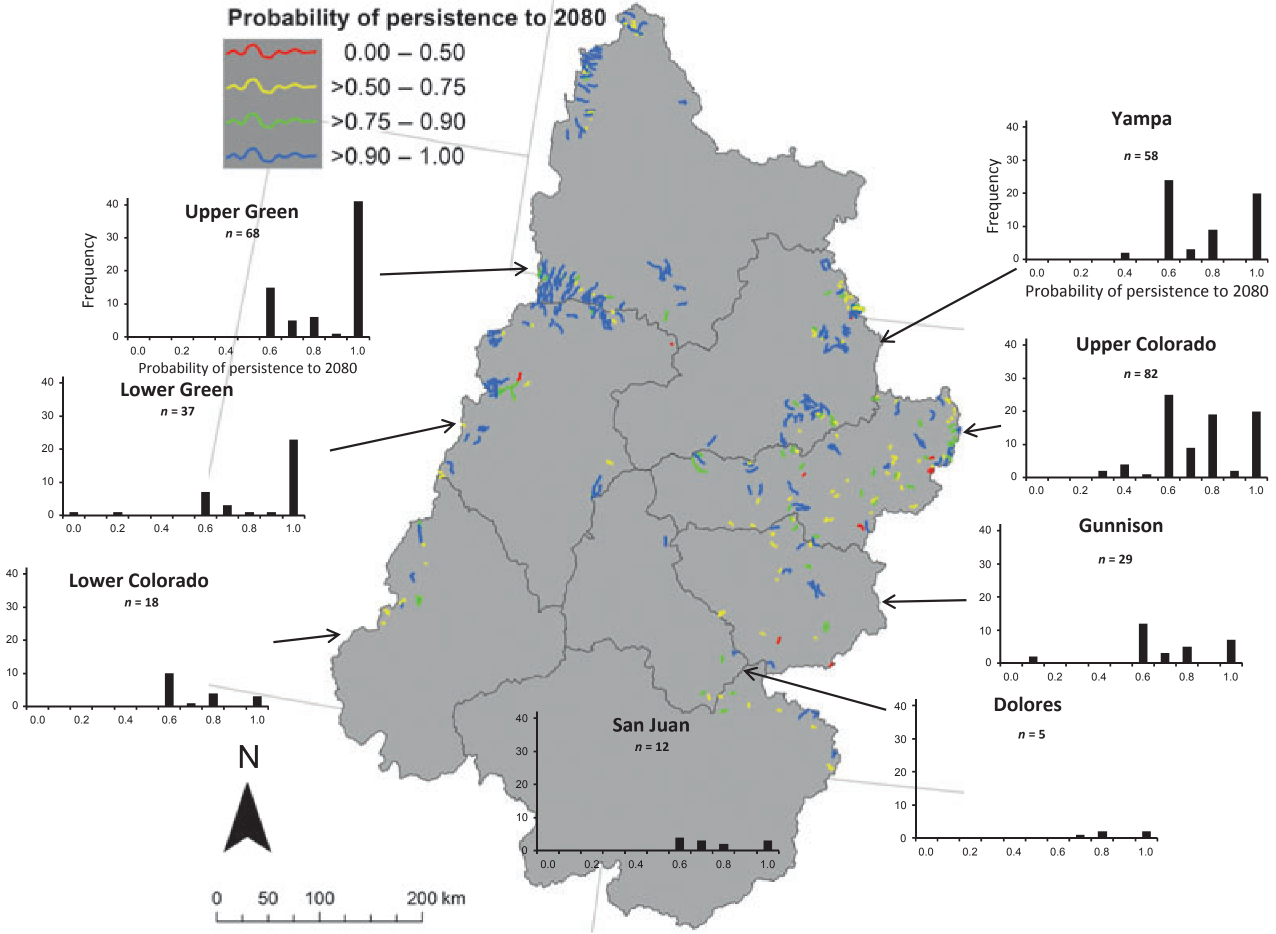

**Fig. 5** The predicted probability of persistence for the 309 conservation populations of Colorado River cutthroat trout (CRCT) to 2080, averaged over both climate models. Colors show the category of persistence probability for each population. The frequency of persistence probabilities for all CRCT populations in each major river basin is summarized in the histograms.

ment, the greater the risk of extirpation for populations as a result of stochastic events or small population size. When we consider both fragment length and stream temperatures and how they interact to influence CRCT population persistence, our BN results indicate that CRCT populations in short fragments of 4 km or less, especially those at lower elevations, are most susceptible to extirpation by 2080. In contrast, populations in fragments of 7 km or longer are predicted to have a high probability of persistence to 2080.

Potential reductions in suitable habitat for salmonids worldwide owing to climate warming have been examined since the 1990s (Nakano *et al.*, 1996), and two early studies predicted substantial decreases (16–72%) in suitable habitat for cold water fishes in the Rocky Mountain region (Keleher & Rahel, 1996; Rahel *et al.*, 1996). These studies assumed a 1–5 °C increase in mean air temperature, and adjusted the range limits of salmonids to higher elevations based on the relationship between elevation, latitude, and air temperature. Flebbe *et al.* (2006) used a similar method and also predicted a large loss of suitable habitat (53–97%) for three species of wild trout in Appalachian Mountain streams.

These studies predicted broad declines in salmonid distributions at lower elevations and latitudes, but other investigators have pointed out that the climate response of salmonids will depend on the ecological setting, and will interact with other aquatic and terrestrial processes. For example, Rieman *et al.* (2007) predicted a 27–99% loss in suitable habitat for bull trout (*Salvelinus confluentus*) in the northern Rocky Mountains with a 0.6–5.0 °C increase in mean air temperature. The reason is that warming water temperatures will restrict bull trout to habitat patches too small in area to support their migratory populations, based on empirical data. Loss of suitable thermal habitat for bull trout, which are among the most sensitive salmonids to warming, can also be exacerbated by land uses like deforestation and natural disturbances such as wildfire (Isaak *et al.*, 2010). In contrast, nonnative rainbow trout (*Oncorhynchus mykiss*), which tolerate warmer temperatures, are less susceptible to such habitat losses in these same basins. In a more sophisticated analysis, Wenger *et al.* (2011) predicted that negative effects of nonnative brook (*Salvelinus fontinalis*), brown (*Salmo trutta*), and rainbow trout will interact with changes in temperature and stream flow, driven by climate change, to reduce available habitat for native cutthroat trout by nearly 60% throughout much of the inland western USA by 2080. Paradoxically, increased winter rain is projected to scour eggs of fall-spawning brook and brown trout from gravel spawning nests, making conditions more favorable for spring-spawning cutthroat trout because they are currently reduced by competition and predation from the nonnative fall-spawning trout (Wenger *et al.*, 2011). Similar to our findings, these studies highlight the importance of including multiple variables in addition to temperature when evaluating the potential consequences of climate change for native fishes.

Our results also indicate that fragment length is an important variable that can interact with the increased environmental variability that will accompany climate change to influence CRCT population persistence. Short stream fragments reduce the potential fish population size by restricting available habitat (Young *et al.*, 2005), placing populations at risk from inbreeding depression and genetic drift. Reducing the available habitat also decreases the amount of refuge habitat, thereby increasing the susceptibility of a population to hazards from stochastic events such as wildfire, debris flows, and stream drying or freezing. These classic threats to the conservation of small populations in fragmented habitats (Caughley, 1994) are accentuated when combined with variability induced by climate change.

Fragmentation has been shown to have catastrophic consequences for populations of native salmonids (Brown *et al.*, 2001; Morita *et al.*, 2009). In Japan, extensive networks of dams in rivers have restricted many populations of charr and landlocked salmon to watersheds of only 1–10 km$^2$ (Morita & Yamamoto, 2002; Endou *et al.*, 2006). This extreme fragmentation is a threat to population persistence owing to the loss of groups of fish with different life history strategies, which leads to reduced numbers of spawning fish, small population sizes, and the loss of potential rescue effects from migratory fish (Morita *et al.*, 2009). Fragmented populations (0.4–6.1 km) of endangered Gila trout (*Oncorhynchus gilae*) have been extirpated during and after wildfires, and remaining populations are at risk from stochastic events (Brown *et al.*, 2001). Short stream fragments increase the risk of extirpation from these stochastic events because they often lack internal habitat refugia found in longer segments (Rieman & Clayton, 1997).

Our models do not predict broad-scale declines in thermal habitat suitability for CRCT in the upper Colorado River basin, as have some previous studies for salmonids in the Rocky Mountain west. This is primarily because the range of CRCT has already been drastically reduced by >80% from invasive trout and land uses that degrade habitat (Hirsch *et al.*, 2006; Young, 2008; Cook *et al.*, 2010). The amount of CRCT habitat already lost is similar to the amount predicted to be lost from future climate change for other salmonids across North America (Flebbe *et al.*, 2006; Wenger *et al.*, 2011). Therefore, our analysis emphasizes the importance of addressing the regional-scale ecological setting (i.e., historical habitat loss) when examining potential impacts of climate change for biological populations.

Although many CRCT populations have already been lost, our modeling indicates that many remaining populations are relatively secure, and suggests promising avenues for future conservation to offset the risks of climate change. For example, the BN predicts that 170 of 309 (55%) CRCT conservation populations have a better than 70% chance of persistence to 2080 (Fig. 5), largely because they occur in stream fragments of sufficient length to buffer against stochastic disturbances. However, a common rule of thumb for conservation biology is that a population is considered vulnerable (as defined by the IUCN) if it has <90% chance of persistence over the next 100 years (Mace & Lande, 1991). Based on this more stringent criterion, only 37% of CRCT populations are secure from extirpation to 2080. Therefore, foremost among management options will be to prevent further fragmentation and habitat loss, and to lengthen fragments, where possible, by removing barriers and nonnative species from adjacent reaches.

Paradoxically, the fact that extant populations of CRCT are restricted to higher elevations and are thereby relatively resilient to warming temperatures gives managers options to increase resilience further by increasing fragment length to buffer against stochastic disturbances. In particular, peripheral populations at the southern extent of CRCT distribution, which we originally predicted would be sensitive to warming, are at high elevations and the chances of persistence for many could be increased if stream fragments were lengthened. In contrast, managers of coldwater aquatic species in other regions may have few options for conserving the remaining populations given the predicted inexorable temperature increases.

Although the BN model projects that temperature increases will be a lesser problem for most CRCT populations than for other native salmonids (e.g., bull charr), it would still be prudent to temper rising stream temperatures by restoring and maintaining channel morphology and riparian vegetation. These actions can protect important groundwater sources and provide shading for lower elevation CRCT streams, which we predict are closer to stressful thermal conditions.

The unique approaches used in our analysis afforded us insights that have not been possible in previous broad assessments of potential climate risks for native salmonids. Specifically, using a large network of local stream temperature data to create a regional stream temperature model, instead of relying solely on air temperature, allowed direct predictions of effects on key life history events like growth, reproduction, and mortality. Likewise, using a spatially explicit database of the entire distribution of CRCT in streams (Hirsch *et al.*, 2006) allowed us to make temperature predictions at the scale of individual stream fragments, and then use these to make empirical predictions of persistence.

Several caveats are important to consider when assessing the accuracy of our model predictions. First, our analysis indicated that the stream temperature model may predict maximum stream temperatures that are several degrees low, so that some stream reaches may be above lethal limits (MWMT > 26.0 °C) even though none were predicted to exceed this threshold. However, only 16% of the 823 NHDPlus reaches and 9% of the 309 CRCT segments were predicted to exceed a lower threshold for MWMT of 23.0 °C by 2080, where underestimates become more frequent, so this inaccuracy apparently had few consequences for our results. Second, we note that the predicted runoff patterns used in these stream temperature models are based on precipitation forecasts from RegCM3, which are more variable across multiple GCMs than the air temperature predictions from these models (Hostetler *et al.*, 2011). A third caveat is that we assumed no change in fragment size over time. If stream drying, new nonnative trout invasions, or changes in human land or water use further reduce the length of fragments, then we predict greater risk for CRCT populations, which our BN model can be used to estimate. Future modeling efforts should focus on the consequences of such increasing fragmentation.

Climate change is a major threat to many aquatic ecosystems and biota, but interactions of these physical changes with other stressors will be of equal or greater importance for biological conservation (Rahel & Olden, 2008). Currently, CRCT occupy a small proportion of their historical range, primarily at high elevations in relatively short stream fragments. Given this ecological setting, it is not surprising that increased water temperatures are not predicted to be a major threat to most populations. However, the interacting negative effects of stochastic risks from wildfire, debris flows, and stream drying and freezing, coupled with small fragment lengths pose a threat for many. Even though we projected persistence for relatively short periods of 30 and 70 years, only 37% of the extant populations met the standard conservation criterion of a $\geq$90% chance of persistence over the longest period modeled (to 2080).

Future CRCT conservation efforts should focus on preventing further loss of habitat from CRCT segments, and expanding segment length for these isolated populations where possible. These efforts could be aided by the tools we developed for this study, including the regional stream temperature model and the BN model of CRCT population persistence. These tools would be particularly useful to evaluate potential future habitat expansions for CRCT and other native salmonids, and can help ensure that limited conservation resources are allocated to habitats best suited for species persistence under changing climatic conditions. Overall, this study highlights that explicitly accounting for interactions between climate change and other components of the ecological setting, like stream fragment length, will be critical when predicting impacts of future climate conditions on imperiled aquatic biota.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Data S1.** Details about methods for fitting the stream temperature model, BN sensitivity analysis, and node state definitions.
**Tables S1–S5**. Conditional probability tables, sensitivity analysis, and details about the Universal Kriging model and stream temperature model output.
**Figures S1–S8**. Details about stream temperature model fit and output.