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Biotic and Abiotic Associations with Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*) in the North Fork Flathead River Basin in northwestern Montana, USA and southeastern British Columbia, CAN under current and future climate scenarios.

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Abstract
Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*; WCT) populations are declining across much of their native range due to threats such as habitat degradation, competition with non-native species, and climate change. Understanding how habitat characteristics impact distributions of nonhybridized WCT populations throughout a relatively pristine core conservation area is needed to inform management and conservation efforts. We investigated whether abiotic (e.g., gradient) and biotic (i.e., Bull Trout – *Salvelinus confluentus*) variables predicted WCT presence and predicted how future stream temperature projections for the area might be expected to alter distributions. We compared logistic regression models of WCT presence throughout tributaries of the North Fork Flathead River in Montana, USA and British Columbia, CAN models using a variety of metrics (e.g., Akaike Information Criterion). WCT were widespread throughout the 293 reaches analyzed (present in 69.3% of reaches). Their presence was predicted by gradient, summer temperature, and an interaction of pool density and Bull Trout. Using this regression model and climate projections under both moderate and extreme emissions scenarios, WCT presence is predicted to increase by 13.0% and 14.1% respectively in 2075 from current distributions based on changes in temperature alone. When changes in Bull Trout distributions and temperatures are considered, WCT distributions are predicted to increase by 13.4% and 17.5% under the moderate and high emissions scenario, respectively. This conservation area is predicted to continue to serve as a WCT stronghold, if other threats can be contained.

Introduction

Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*; hereafter WCT) is a native salmonid species of conservation concern in the Rocky Mountain west as its populations are declining across much of their native range due to a number of threats such as invasive hybridization with introduced Rainbow Trout *Oncorhynchus mykiss;* RBT), habitat degradation and fragmentation, competition with non-native species, and climate change (Muhlfeld et al. 2016). Many of these threats are interrelated and their impacts on WCT can be additive. For example, in addition to decreasing the amount of suitable habitat available to WCT based on physiological tolerances (Wenger et al. 2011), warming stream temperatures can also accelerate invasive hybridization with RBT (Muhlfeld et al. 2014). Nonhybridized populations of WCT make up a small portion of their native range, less than 10% in the United States and less than 20% in Canada (Muhlfeld et al. 2009). Habitat loss from activities such as dam construction, irrigation diversions, and improperly sized culverts, has occurred throughout WCT's historical range (Young 1995). This fragmentation is especially detrimental to the migrant members of WCT populations by restricting their ability to move through river systems. Additionally, Young (1995) suggests that the loss of these migratory life forms within a WCT population (via a lack of gene flow between migratory and resident trout) may decrease the persistence of these populations across their range.

As we work to conserve WCT, it is critical to understand how habitat characteristics (e.g., stream temperature) impact distributions of nonhybridized populations of WCT throughout relatively pristine ecosystems (e.g., North Fork Flathead River system) to inform management and conservation efforts for

WCT in these systems and elsewhere in their range. Ecologically, WCT have fairly specific habitat requirements typically inhabiting cold, waters with low nutrient concentrations (Shepard et al. 2005, McIntyre & Rieman 1995) and historically connected habitat (D'Angelo et al. 2015). WCT require cooler streams so stream temperature is an important factor in determining habitat suitability for WCT (McIntyre & Rieman 1995, Bear, McMahon & Zale 2007, Rasmussen, Robinson, & Heath 2010, D'Angelo & Muhlfeld 2013, Yau & Taylor 2014). WCT have reduced growth and are more susceptible to mortality at high stream temperatures (Bear et al. 2007, Wegner et al. 2011). Specifically, Bear et al. (2007) found in laboratory studies that while WCT and introduced RBT have similar peak optimum growth temperatures, both the upper ultimate incipient lethal temperature and overall thermal optimum growth range for WCT is much lower and narrower than it is for RBT. Given these temperature requirements understanding current predictors of habitat suitability to predict how future distributions may change with warming stream temperatures is needed to inform habitat protection and restoration.

The North Fork (NF) Flathead River Basin runs to the northern portions of Montana, USA from British Columbia, CAN and is recognized as a stronghold for nonhybridized WCT (D'Angelo et al. 2015). The importance of this area for WCT conservation has given rise to several important studies within the last 10 years (e.g., Muhlfeld et al. 2009, D'Angelo & Muhlfeld 2013, D'Angelo et al. 2015, and Jones et al. 2017). Muhlfeld et al. (2009) focused on the influence of abiotic and biotic factors on WCT hybridization with RBT in the upper NF Flathead River system to help identify areas at risk of introgression. D'Angelo & Muhlfeld (2013) identified key habitat characteristics, such as August mean stream temperature, large woody debris (LWD) density, and pool density on WCT and Bull Trout (*Salvelinus confluentus*; BT) distributions throughout Glacier National Park (near the lower end of the NF Flathead R. basin). Examining the generality of these results across the broader basin is needed for conservation actions beyond Glacier National Park.

In this study we assessed how WCT distributions in tributaries of the NF Flathead River are currently related to habitat characteristics and how warmer stream temperatures could change these distributions under future climate scenarios. Specifically we addressed:

(1) What abiotic and biotic factors predict WCT presence in the tributaries of the North Fork Flathead River?

(2) How might WCT distributions change under future climate scenarios?

We predicted future distributions using two different emissions scenarios for this region (Jones et al. 2017) and given the results from the first analyses we considered two scenarios for drivers of change in future distribution (abiotic only or abiotic and biotic). The first scenario only included changes in abiotic factors, specifically modeling how changes in stream temperatures alone will affect future WCT distributions based on physiological tolerances. The second scenario considered changes in stream temperatures and biotic interactions (specifically potential reach-scale release from competitive exclusion). Araújo & Luoto (2007) support including small-scale biotic interactions, because they can significantly improve the predictive power of species distribution models at the landscape scale. In addition to previous research that suggests resource partitioning (Nakano et al. 1992), there was a negative-reach scale association between WCT and BT our data set. Therefore, we included this consideration in the second scenario to assess how WCT distributions might change if BT are currently excluding WCT from reaches that might open up for WCT as they become unsuitable for BT under future stream conditions.

Materials and methods

Study Area

The North Fork Flathead River basin is located within the Crown of the Continent Ecosystem (CCE, 72,000 km^2) (Jones et al. 2017). Our study area encompasses approximately 16,000 km^2 and includes 49 tributaries from a total of 27 sub-drainages in the northern portion of the NF Flathead River basin in British Columbia, CA and the southeastern portion in Glacier National Park, Montana, USA (Figure 1). This is a snowmelt driven hydrograph with high peak spring flows as the snowpack melts (USGS 2016 – Station 12355000) and August mean air temperatures have averaged 15ºC over the last decade (2008-2018) (calculated from decadal August air temperature averages sourced from NWRFC 2010 and NRCSa-d). The area is considered an important core connected conservation area for WCT as they are widespread, current August mean stream temperatures rarely exceed 14ºC, and it supports the diversity of resident and migratory life history types (D'Angelo et al. 2015).

Fish distribution, habitat variables, and temperature projections for analyses

Field crews from Montana Fish, Wildlife & Parks (FWP) and the Northern Rocky Mountain Science Center of the United States Geological Survey (USGS) collected the fish distribution and habitat data via systematic surveys throughout sub-drainage streams and tributaries from 2008-2012 during the months of July through September. The reaches were located approximately 1km apart and surveyed with single-pass upstream backpack electrofishing surveys as far upstream as logistically possible. Depending on the reach, either one or two backpack electrofishing units were used during daylight hours at or near base flow conditions (Smith-Root Model L-24, Vancouver, Washington; 30-50 htz, 3 ms pulse width, 300-700 volts). Each reach began at a pool on the downstream edge and continued upstream to a natural barrier (e.g., riffle, large woody debris (LWD) aggregate). Reach lengths ranged from 20 m to 203 m. (D'Angelo & Muhlfeld 2013, D'Angelo et al. 2015)

Fish species, total lengths, and numbers captured were noted for each reach. The detection of BT was included as an independent variable, while the detection of WCT was used as the dependent variable (presence = "1", absence = "0"). Given the influence of different habitat features on the detection probabilities of WCT abundances using single-pass electrofishing, we chose to use presence/absence data for our analyses versus relative abundance (Kruse et al. 1998), as WCT has been shown to have high (0.91, range 0.87-0.97) detection probability for presence/absence with various sites characteristics and crews (LeMoine et al. in prep). Habitat data collected at each reach included: elevation, average gradient, stream width, substrate, number of LWD pieces, and number of pools. We calculated the average gradient values in ArcGIS with the Add Surface Information tool via 10m resolution digital elevation models of the study area. If we were unable to calculate average gradient in ArcGIS, we used the values collected in the field.

We excluded the reach data from analyses if the reaches were located upstream of known absolute barriers to fish movement (n = 26), dewatered or the stream went subsurface within the reach (n = 2), if only migratory (i.e., fork lengths greater than 250 mm) WCT and/or BT individuals were present (n = 2), if the reach was located below a lake stocked with WCT (n = 1), if trout were seen, but not netted and/or detection issues were suspected due to habitat features (i.e., deep pool) (n = 4), or if there was missing habitat data (n = 13). After excluding these data, we had a total of 293 reaches included in our analyses.

We used the stream temperatures modeled by Jones et al. (2017) under base conditions and two emission scenarios, representative concentration pathways (RCP) 4.5 and 8.5 into 2035 and 2075 for the Crown of the Continent Ecosystem. Their seasonal models were built on a large assemblage of empirical bi-hourly stream temperature readings, with six fixed effect covariates (air temperature, elevation, slope, lake presence, glacier presence, and month) and one random effect (watershed unit). They chose the best

model via internal cross-validation and noted that the model performed well even in years that experienced global air temperature anomalies. They found that the summer months (July, August, and September) were predicted to experience the greatest changes is mean monthly temperatures. Therefore, we chose to use temperature predictions for August, because those represent the most extreme upper temperatures that WCT will experience under future conditions.

Delineation of thermal thresholds

For WCT, we incorporated both upper and lower thermal thresholds. We chose 6ºC to be the lower threshold because the reach with the coldest temperature used by WCT in this electrofishing data set was 6.4ºC. The current summertime maximum temperatures in this data set were below 15.3ºC. We used 18ºC as the upper threshold, because that was the warmest temperature WCT were recorded to experience in the radio telemetry data collected by D'Angelo et al. (2015) between 2012-13 in the months of July and August. This value also corresponds with the temperature at which Bear et al. (2007) found WCT survival begins to decrease in their lab studies. We included an upper thermal threshold for BT at 14ºC. This value is based off of the warmest stream temperature predictions where BT were detected (~13.9ºC) and is consistent with the upper limits found in Jones et al. (2014).

Statistical Analyses

All of our statistical analyses were conducted in RStudio (v.1.1.456, R Core Team 2018). We used a mixed effects logistic regression model structure to predict WCT presence or absence under current and future stream temperature predictions using the lme4 package (Bates et al. 2015). We analyzed five fixed effects variables: temperature (ºC, from the base temperature predictions in Jones et al. (2017) model), average gradient (%), pool density (number of pools/100 m^2), LWD density (number of LWD pieces/100m^2), and BT presence. We didn't include substrate as a fixed effect, because there were no major differences in WCT use across the different substrate types. Elevation was highly correlated with temperature (Pearson's $r = - 0.77$) and was therefore dropped from the analysis. All other variables were uncorrelated (Pearson's $r < |0.7|$). Stream was included as a random effect to account for spatial autocorrelation between reaches located within the same stream.

We created candidate models from various combinations of these fixed effects. As BT is a biotic variable and thus is likely influenced by abiotic variables itself, we also considered interactions between BT and temperature, LWD, and pool density. We chose our top model using a variety of metrics: Akaike Information Criterion (AIC), area under the receiver operating characteristic curve (AUC), sensitivity, specificity, and positive predictive values. We determined the optimal threshold for assigning predictions as a presence or absence by finding the threshold that maximized the sum of the sensitivity, specificity, and the positive predictive value. We also conducted an internal cross-validation by randomly selecting 75% of the dataset to train the model and validating on the remaining 25% of the data. From this cross-validation dataset we calculated AUC, misclassification rates, sensitivity, specificity, and positive predictive values. Lastly, we calculated the marginal and conditional R^2 values to assess the effect of including stream as a random effect using the sjstats package in R (Lüdecke 2019).

Application of Species Distribution Model (SDM)

Once we determined the top model, we took the predicted probabilities for each temperature scenario (base, RCP 4.5 – 2035, RCP 4.5 – 2075, RCP 8.5 – 2035, RCP 8.5 – 2075 from Jones et al. 2017) and ran them through an if/then framework based on each scenario. Under the if/then framework for the abiotic only predictions: if the model predicted a presence (i.e., the probability of occurrence was greater than the optimal threshold), the predicted stream temperature for that reach was greater than or equal to 6ºC, and less than or equal to 18ºC, that prediction remained a presence. If the predicted stream temperature was outside of that range, the prediction changed to an absence. For the release of the competitive exclusion prediction scenario, we imposed temperature thresholds for BT by changing any presence to an absence if the predicted temperatures exceeded 14ºC. The WCT predicted probabilities for

each temperature scenario included the predicted BT presence for each site and the temperature scenario followed the same if/then framework as described above.

Results

Study Area Attributes

WCT were present in 203 of 293 reaches (69.3%), BT were present in 62 of 293 reaches (21.2%), and WCT and BT were present in sympatry in 31 of 293 reaches (10.6%) throughout the study area. While WCT were found in 50% of the reaches where BT were present, when the two species were detected in sympatry, one or both species were present in low densities (Figure 2). The mean elevation was 1446 m (2*Standard Error, S.E. = ± 23 m) and ranged from 596 m to 2027 m. The mean stream gradient was 4.0% (± 0.9% 2 S.E.) and ranged from 0% to 30.8%. The mean pool density was 1.5 pools/100m^2 (± 0.5 pools/100m^2 2 S.E.) and ranged from 0 to 16.2 pools/100m^2. The mean LWD density was 1.6 pieces/100m^2 (± 0.9 pieces/100m^2 2 S.E.) and ranged from 0 to 55.6 pieces/100m^2.

Model Selection

The top model included temperature, average gradient and an interaction between BT and pool density. Average gradient and BT were consistently included as significant ($p < 0.05$) negative predictors of WCT presence in the top models by AIC (Table 1.) The marginal R^2 of the top model was 0.144, whereas the conditional R^2 considering the random effect of stream was 0.463. Pool density alone was never a significant predictor, but the interaction between pool density and BT was consistently included in the top models as a significant ($p < 0.05$) positive predictor of WCT presence. In the top model, temperature was a positive predictor and nearly significant ($p = 0.07$). LWD was a positive predictor of WCT, but was rarely included in the top models and was never significant. We chose an optimal threshold for our probability of WCT being present of 0.721 to delineate presences and absences from the predicted probabilities of WCT presence, because that value maximized the sensitivity, specificity, and positive predictive value of the model.

Future Predictions

WCT distributions increased from base predictions under all emissions and biological scenarios. Under the moderate emissions (RCP 4.5) and abiotic only scenario, WCT distributions increased by 4.5% and 7.8% from base predictions into 2035 and 2075 respectively. Under the moderate emissions and release from competitive exclusion scenario, WCT distributions increased by 5.2% and 8.1% from base predictions into 2035 and 2075 respectively. Under the high emissions (RCP 8.5) and abiotic only scenario, WCT distributions increased by 13.0% and 14.1% from base predictions into 2035 and 2075, respectively. Under the high emissions and release from competitive exclusion scenario, WCT distributions increased by 13.4% and 17.5% from base predictions into 2035 and 2075, respectively. The model tended to under predict WCT presence under all scenarios, and increases in distributions past the observed WCT prevalence didn't occur until 2075.

Under the abiotic only scenario, 83.3% of reaches (244) remained either a presence or absence, 10.2% of reaches (30) were predicted to gain WCT, and 6.5% (18) of reaches were predicted to lose WCT when compared with the original observed values under the moderate emissions (RCP 4.5) scenario into 2075. The gained and lost reaches fell within nearly the same mean predicted temperatures of 12.0ºC (± 0.6ºC 2 S.E.) and 12.1ºC (± 1.0ºC 2 S.E.) and relatively similar elevations of 1472m (± 84m 2 S.E.) and 1427m (± 80m 2 S.E,), respectively (Fig. 4b, 4e). Under the high emissions (RCP 7.5) scenario, 78.8% of reaches (231) were predicted to remain the same as the observed values, 13.0% (38) were predicted to gain WCT and 8.2% (24) were predicted to lose WCT into 2075. The gained reaches tended to fall within cooler predicted temperatures (13.6 ± 0.4ºC 2 S.E.) and higher elevations (1481 ± 69m) than the lost reaches, which tended to be warmer (16.9 ± 1.1ºC 2 S.E.) and at lower elevations (1254 ± 65m) (Fig. 4c, 4f).

Under the release from competitive exclusion scenario, 83.6% of reaches (245) were predicted to remain consistent with the observed WCT presences/absences, 10.2% of reaches (30) were predicted to gain and 6.1% (18) were predicted to lose WCT according to the moderate emissions scenario into 2075. All of the predicted gains in WCT were attributed to changes in temperatures, rather than a loss of BT and had the same mean predicted temperatures and elevations as were noted under the temperature only scenario. Under the high emissions scenario, 77.5% of reaches (227) were predicted to remain consistent with observations, 15.4% (45) were predicted to gain WCT, of which 20.0% (9) coincided with BT losses, and 7.2% of reaches (21) were predicted to lose WCT into 2075. The reaches with WCT gains attributed solely to temperature tended to occur at lower temperatures (13.6 ± 0.4ºC 2 S.E.) and higher elevations (1485 ± 73m 2 S.E.). Whereas reaches that gained WCT and simultaneously lost BT occurred at mid-temperatures (14.6 ± 0.3ºC 2 S.E.) and mid-elevations (1337 ± 36m 2 S.E.). Reaches that lost WCT occurred at the warmest mean temperatures (17.3 ± 1.2ºC 2 S.E.) and lowest elevations (1246 ± 70m 2 S.E.) (Fig. 5a, 5b).

Discussion

The North Fork Flathead River basin has previously been identified as a core conservation area for WCT (D'Angelo et al. 2015). Considering the predicted stream temperature increases into the future, we expect this area to continue to serve as an important thermal refuge for WCT, with our model predicting WCT distributions to increase across all scenarios.

As we consider interpreting and acting upon species distribution models for highlighting areas for conservation now and into the future, it is important to consider major assumptions. Dormann (2007) outlined three assumptions for extrapolating SDM predictions into the future: 1) factors currently limiting species distributions will continue to do so, 2) genetic variability and phenotypic plasticity are negligible, and 3) biotic interactions will remain the same. Our model complies with the first two assumptions as two of the main factors affecting WCT presence in our model are related to physiological constraints (i.e., average gradient and temperature). Average gradient of the stream reaches is a fairly stable environmental condition and is unlikely to change into the future. Thus, WCT's physiological ability (or lack thereof) to reside in streams of a certain gradient is likely to remain constant into the future. WCT are ectotherms and cold-water specialists, so their presence will always be somewhat reliant on stream temperature. Our predictions account for this factor by imposing upper and lower thermal limits on the reaches WCT can be predicted present in. Additionally, as most tributaries in the NF Flathead River are predicted to remain fairly cold (i.e., < 18ºC), we would expect WCT thermal tolerances to remain the same into the future. Similar to average gradient, pool density is expected to remain the same under future scenarios. However, if the effect of pool density on WCT presence is more impactful when BT presence is considered (our interaction term), then WCT might respond differently to pool density if BT can no longer tolerate the warmer (i.e., > 14ºC) stream temperatures. Likewise, the influence of BT on WCT presence is likely to change as reaches thermally suitable for BT decrease. We tried to account for these potential assumption violations under our release of *competitive exclusion* scenario, as we imposed thermal restrictions on BT presence in these predictions. Given that the temperature range remains within the current known regional range of WCT, there is no need to make assumptions regarding plasticity, natural selection or genetic variation for its future distribution. The prediction of the loss of BT in reaches that exceed 14°C has been documented in Montana watersheds across much of the range of BT that state (Al-Chokhachy et al. 2016) as well as this basin (Jones et al. 2014).

The third assumption (i.e., biotic interactions remain constant) is likely the most strained as we predict WCT presence into the future. As noted above, we attempt to account for the changes in BT presence with our *release from competitive exclusion* scenario prediction restrictions, but we are unable to account for other biotic interactions (e.g., non-native species encroachment). When these data were collected, only native species were documented in the British Columbia portion of the study area and few non-native species were found in the GNP portion of the study area. As stream temperatures warm, non-

native species such as RBT are able to expand their range, which will likely increase competition for WCT and threats of hybridization (Muhlfeld et al. 2014). However, in upper reaches that are predicted to remain colder than RBT can tolerate, biotic interactions are expected to remain the same. Continuing the efforts that are working to manage the hybridization threat in this basin is critical for maintaining its role as a WCT stronghold into the future (Boyer et al. 2008, Steed et al. 2009)

Most of the covariates included in our final model coincided with previous literature assessing important habitat characteristics for WCT and closely related subspecies. Several studies have documented the influence of stream temperature on habitat suitability for WCT (McIntyre & Rieman 1995, Bear, McMahon & Zale 2007, Rasmussen, Robinson, & Heath 2010, D'Angelo & Muhlfeld 2013, Yau & Taylor 2014). The temperature coefficient included in our final model, was nearly significant ($p = 0.08$) and was positive, likely because the majority of stream temperatures remained within WCT thermal tolerances. The increasing stream temperatures also appear to open up more potential habitat for WCT at the upper edges of their range Fig. 4f). Interestingly, the mean predicted August temperature at newly gained reaches (13.6 ± 0.4ºC 2 S.E.) coincided with the peak daily thermal growth optima for WCT identified by Bear et al. (2007, 13.6ºC).

In contrast with our results, D'Angelo & Muhlfeld (2013) only included stream gradient in one of their top models as a positive predictor of WCT presence; whereas stream gradient was included in all of our top models as a significant, negative predictor of WCT presence. The discrepancy in these results is likely a result of overall differences in gradient between GNP and the British Columbia reaches. For instance, if the changes in gradient are less severe in GNP, they might not have as much of an influence on WCT habitat use as compared to when all of the British Columbia sites are considered with the GNP data.

Pool density has also been commonly found to influence WCT and other closely related subspecies habitat use (Rosenfeld et al. 2000, Rosenfeld & Huato 2003, Young 1996). However, pool density alone explained little in our dataset until BT presence was also included as an interaction. Specifically, when BT were present, increases in pool density dramatically increased the probability of WCT presence at a given site. Very few studies have previously included native:native species interactions in a SDM as we did by including BT presence, although some studies have considered the influence of exotic species as a predictor of native fish distributions. BT presence itself was a significant negative coefficient as we expected given the negative reach-scale association noted by D'Angelo & Muhlfeld (2013) and see overall in our data (Fig. 1). Additionally, the evidence of resource partitioning between WCT and BT in the NF Flathead River provided in Nakano et al. (1992) suggests that BT could either be excluding WCT from deep, covered pools or their presence indicates some set of habitat characteristics less favorable for WCT use. In either case, it is beneficial to include BT presence as a predictor of WCT presence.

The tendency of our top model to under predict WCT presence is likely a result of several ecological factors we couldn't incorporate into our model. For example, WCT have a relatively patchy distribution throughout the study area, and our model likely struggled to accurately predict WCT presence in the sub-optimal habitat patches where they are currently observed. Additionally, while we were able to control for possible migratory WCT, we were unable to consider intraspecific competition or variation in habitat use among different WCT life stages, which may have influenced our predictive power in less generally optimal habitats. Nevertheless, we still predicted increases in WCT distribution across all scenarios, so if anything our estimated WCT range expansions are conservative.

Considering either the abiotic only or the release from competitive exclusion scenario it is important to note the reach-level characteristics (e.g., stream temperature predictions, elevation) of the sites gaining or losing WCT to better understand how their distributions are shifting with a changing climate. In either scenario, reaches gaining WCT tend to be at cooler temperatures and higher elevations than the reaches

losing WCT (Fig. 4b-4f). The reaches gaining WCT and losing BT are typically occurring at mid-level temperatures, still well within WCT tolerances, but just above the thermal tolerance of BT and mid-elevations in relation to the rest of the study area (Fig. 5a-5b). Broadly, the large proportion of sites predicted to remain consistent with current observations of WCT presence suggests that the North Fork Flathead River basin is likely to continue to serve as a thermal refuge and stronghold for WCT under future climate scenarios. However it is also important to note that within the basin, high elevation sites will be especially important for protection as new habitat opens up for WCT in those areas. Likewise, management efforts may need to be focused on the low elevation sites, which are most at risk of non-native species invasions into the future.

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Figures

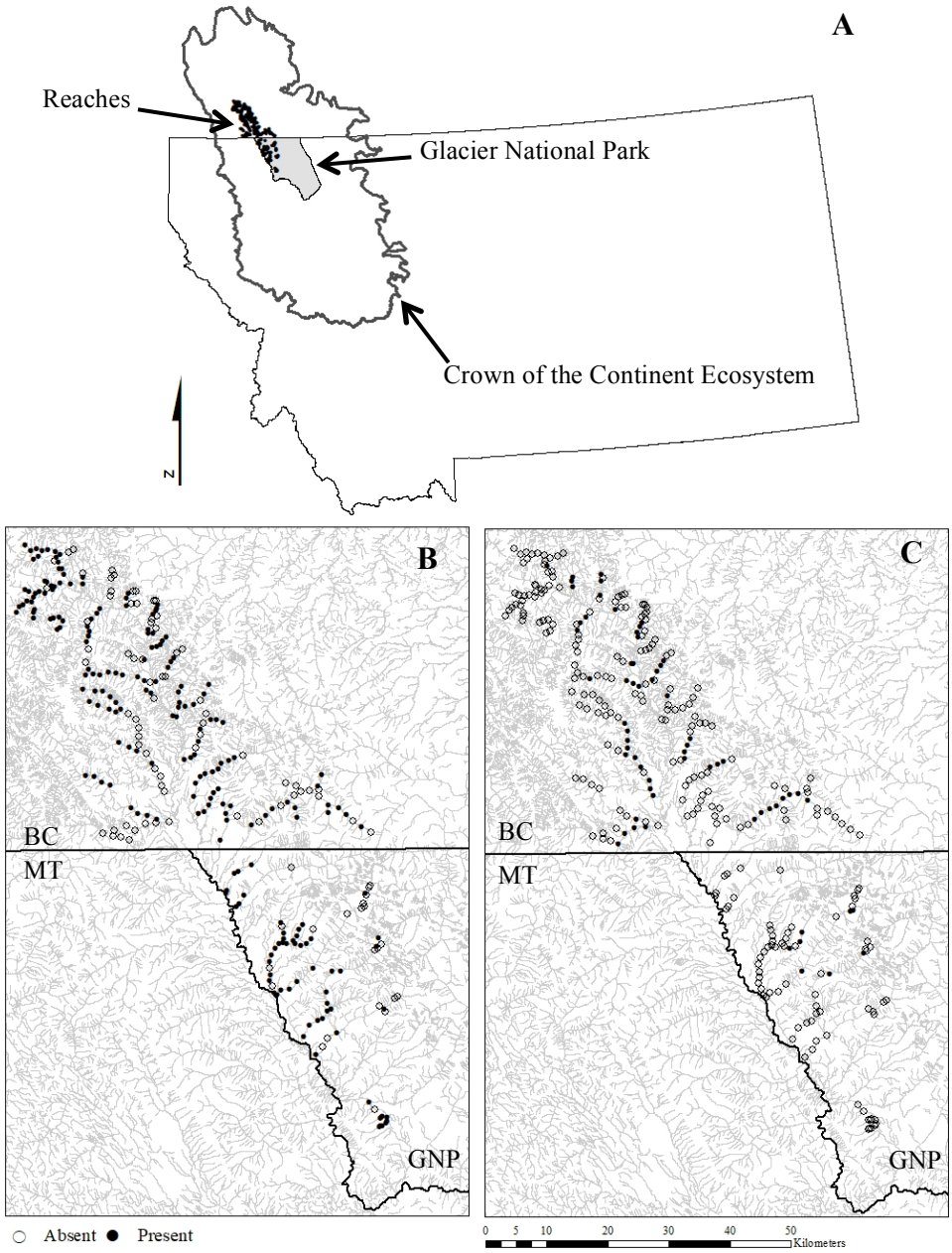


Figure 1. Map of the study area within the North Fork Flathead River basin. (A) Reach locations within the Crown of the Continent Ecosystem in Glacier National Park (GNP) of Montana, USA (MT) and British Columbia, CAN (BC). (B) Presences (filled circles) and absences (open circles) of Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*) and (C) Bull Trout *(Salvelinus confluentus*) throughout the study area.

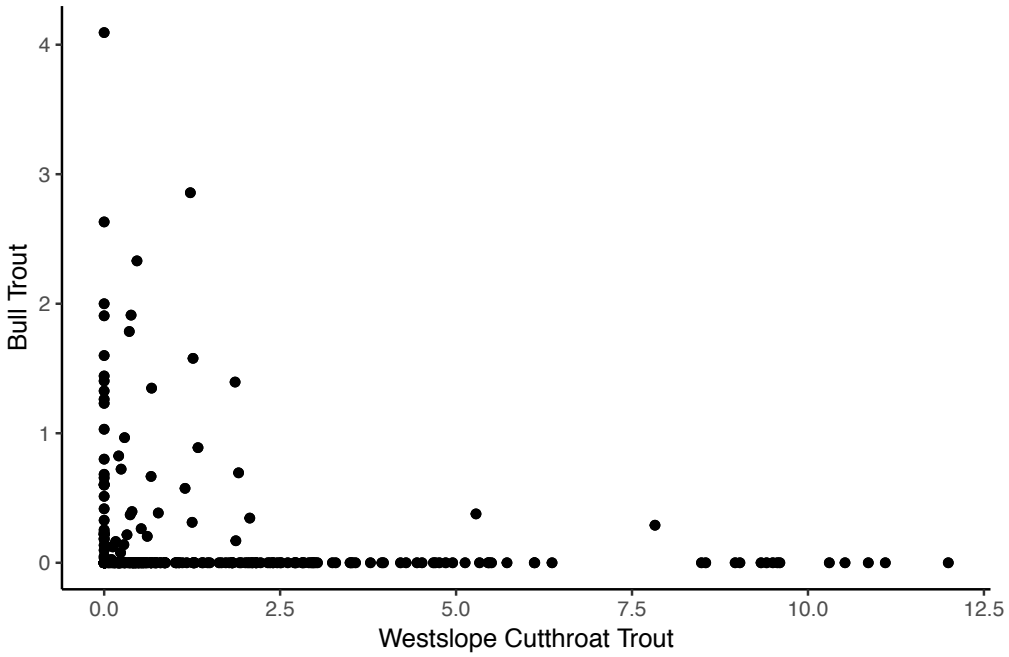


Figure 2. Bull Trout density by Westslope Cutthroat Trout density (number/100m^2) throughout the study area.

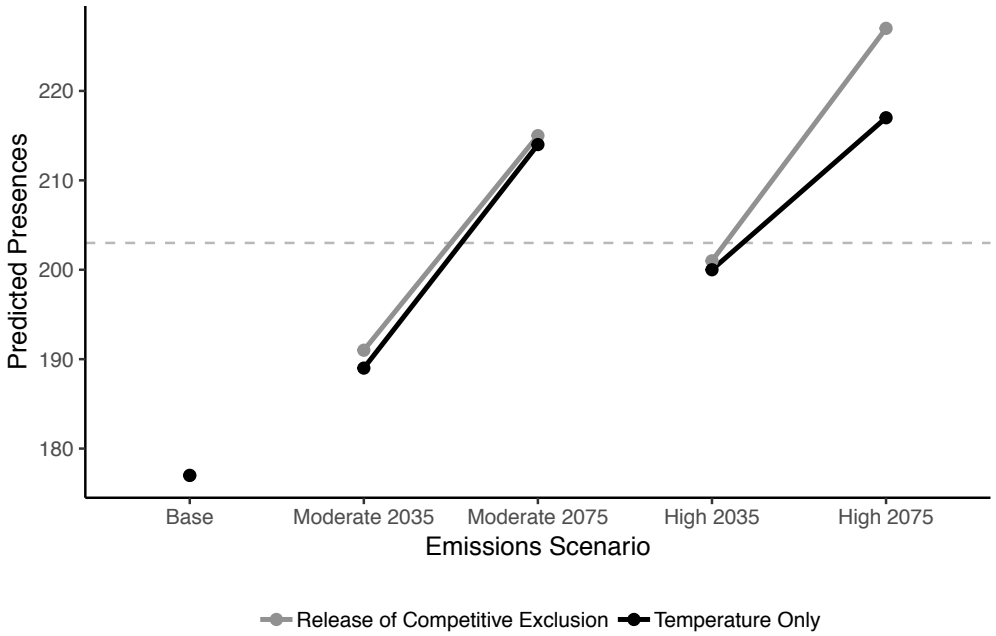


Figure 3. A comparison of WCT prevalence predictions between the temperature only (black) and release from competitive exclusion (gray) scenarios under the moderate (RCP 4.5) and high (RCP 8.5) emissions into 2035 and 2075. Observed WCT prevalence (n = 203) is denoted by the dashed, gray line.

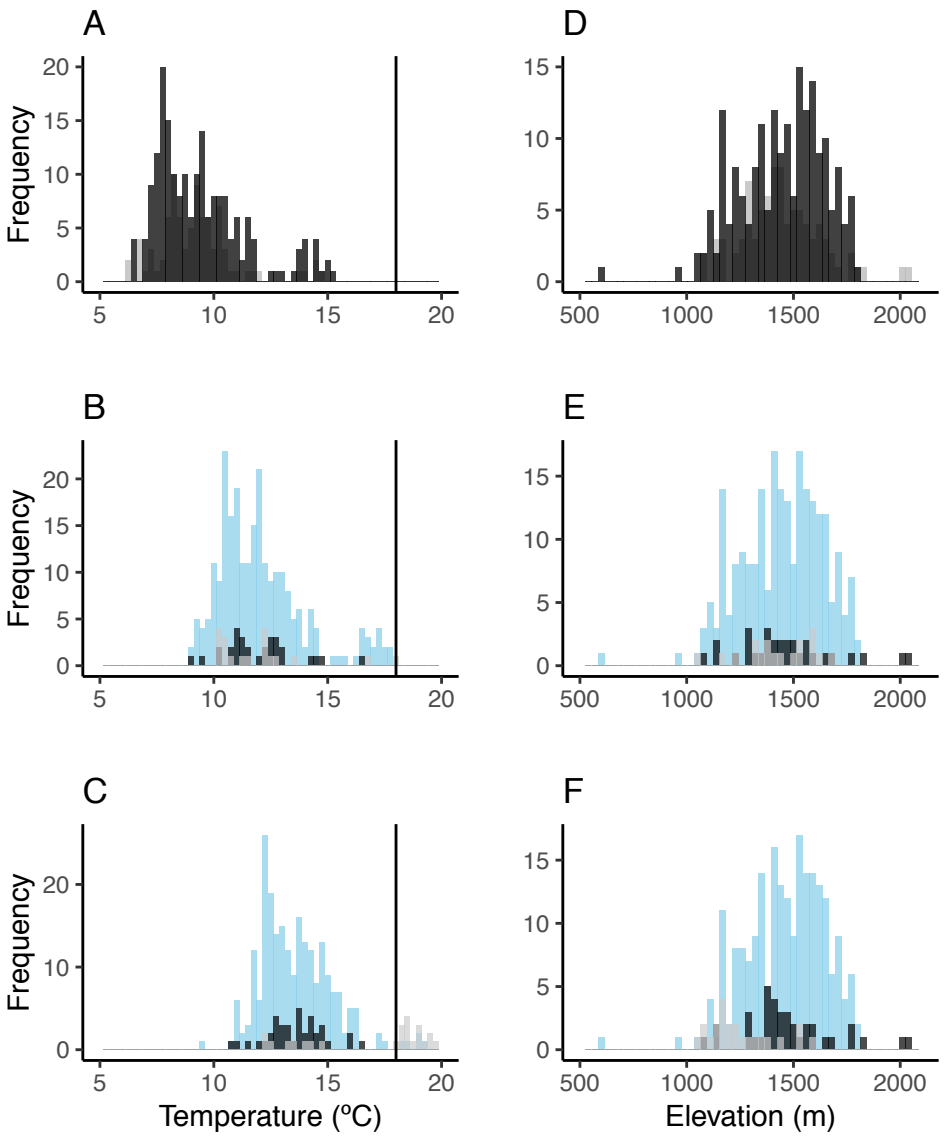


Figure 4. Frequency of observed WCT prevalence (light gray = absence, dark gray = presence) by temperature, ºC (A) and elevation, m (D). Density of reaches predicted to gain (dark grey), lose WCT (light grey), or no change occurred (blue) by temperature (B,C) and elevation (E, F), under the RCP 4.5 emissions scenario (B,E) and the RCP 8.5 emissions scenario (C,F) into 2075. A solid black line denotes 18ºC (the upper WCT thermal threshold), on the temperature graphs (A-C). The elevation graphs (D-F) only consider sites where elevation data was available (n = 280).

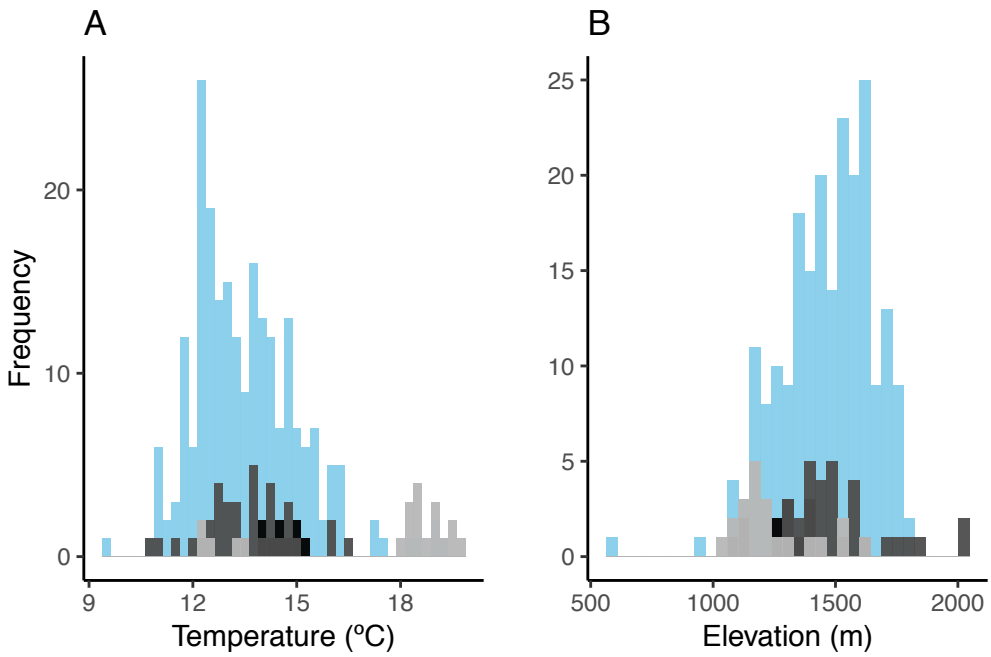


Figure 5. Frequency of reaches predicted to gain WCT where BT are lost (black), gain WCT where BT are not affected (dark grey), lose WCT (light grey), or no change occurred (blue) by temperature ºC (A) and elevation, m (B) under the high (RCP 8.5) emissions scenario into 2075. The elevation graph (B) only considers sites where elevation data was available (n = 280).

Table 1. Model selection results for a mixed effects logistic regression analysis of biotic and abiotic factors predicting WCT presence. BT presence was the biotic factor included. The abiotic factors were mean predicted August temperature (base conditions from Jones et al. 2017), pool density (# pools/m^2), LWD density (# pieces/100m^2) and average gradient (%). Coefficients and area under the receiver operating characteristic curve (AUC) for the overall data (*All*) and an internal cross-validated subset of data (*CV*) were reported for all models with a ΔAIC < 2.00. Significant coefficients are denoted with ** (<0.01) and * (<0.05) and are bolded.

				All	*CV*
Candidate Models + (1|Stream_ID)	**AIC**	**ΔAIC**	**Coefficients**	**AUC**	**AUC**
Temp, Pools, **BT**, Gradient****, **Pools:BT***	317.6	0.0	0.23, 0.08, **-2.29, -0.15**, **2.56**	0.88	0.79
Temp, Pools, BT, **Gradient****, **Pools:BT*,** Temp:BT	318.8	1.2	0.20, 0.07, -5.27, **-0.15**, **2.99**, 0.29	0.88	0.79
Pools, **BT****, **Gradient****, **Pools:BT***	319.1	1.5	0.05, **-2.18**, **-0.17**, **2.36**	0.86	0.79
Temp, Pools, **BT***, **Gradient****, **Pools:BT*,** LWD	319.5	1.9	0.23, 0.07, **-2.27**, **-0.15**, **2.55**, 0.02	0.88	0.78
Temp, Pools, BT, **Gradient****, **Pools:BT1***, LWD, Temp:BT,	320.7	3.1			
Temp, **BT***, **Gradient****	321.9	4.3			
Global - All predictors	322.2	4.6			
Temp, Pools, **BT***, **Gradient****	323.0	5.4			
Temp, **BT***, **Gradient****, LWD	323.6	6.0			
Pools, **BT***, **Gradient****	323.8	6.2			
Null	332.6	15.0			

Table 2. Model selection results for a mixed effects logistic regression analysis of biotic and abiotic factors predicting WCT presence. BT presence was the biotic factor included. The abiotic factors were mean predicted August temperature (base conditions from Jones et al. 2017), pool density (# pools/m^2), LWD density (# pieces/100m^2) and average gradient (%). Coefficients and area under the receiver operating characteristic curve (AUC) for the overall data (*All*) and an internal cross-validated subset of data (*CV*) were reported for all models with a ΔAIC < 2.00. Significant coefficients are denoted with ** (<0.01) and * (<0.05). Continuous variables are scaled with a mean of 0 and a standard deviation of 1.

				All	*CV*
Candidate Models + (1|Stream_ID)	**AIC**	**ΔAIC**	**Coefficients**	**AUC**	**AUC**
Temp, Pools, BT, **Gradient****, **Pools:BT***	317.6	0.0	0.44, 0.15, 1.69, **-0.58**, **5.00**	0.88	0.79
Temp, Pools, BT, **Gradient****, **Pools:BT***, Temp:BT	318.8	1.2	0.38, 0.13, 2.08, **-0.63**, **5.83**, 0.56	0.88	0.79
Pools, BT, **Gradient****, **Pools:BT***	319.1	1.5	0.09, 1.50, **-0.63**, **4.62**	0.86	0.79
Temp, Pools, BT**, Gradient****, **Pools:BT***, LWD	319.5	1.9	0.44, 0.13, 1.70, **-0.59**, **4.98**, 0.08	0.88	0.78
Temp, Pools, BT, **Gradient****, **Pools:BT1***, LWD, Temp:BT	320.7	3.1			
Temp, **BT***, **Gradient****	321.9	4.3			
Global - All predictors	322.2	4.6			
Temp, Pools, **BT***, **Gradient****,	323.0	5.4			
Temp, **BT***, **Gradient****, LWD	323.6	6.0			
Pools, **BT***, **Gradient****	323.8	6.2			
Null	332.6	15.0			

Table 3. Overall and cross-validated misclassification rates (MCR), sensitivities, specificities, and positive predictive values (PPV) for the top model using a threshold of 0.721 to delineate presences and absences.

	MCR	**Sensitivity**	**Specificity**	**PPV**
Overall	0.212	0.800	0.877	0.898
Cross-validated	0.176	0.878	0.720	0.860