

ECOLOGY

Climate change and expanding invasive species drive widespread declines of native trout in the northern Rocky Mountains, USA

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Climate change and invasive species are major threats to native biodiversity, but few empirical studies have examined their combined effects at large spatial and temporal scales. Using 21,917 surveys collected over 30 years, we quantified the impacts of climate change on the past and future distributions of five interacting native and invasive trout species throughout the northern Rocky Mountains, USA. We found that the occupancy of native bull trout and cutthroat trout declined by 18 and 6%, respectively (1993–2018), and was predicted to decrease by an additional 39 and 16% by 2080. However, reasons for these occupancy reductions markedly differed among species: Climate-driven increases in water temperature and decreases in summer flow likely caused declines of bull trout, while climate-induced expansion of invasive species largely drove declines of cutthroat trout. Our results demonstrate that climate change can affect ecologically similar, co-occurring native species through distinct pathways, necessitating species-specific management actions.

INTRODUCTION

Climate change and invasive species are leading causes of global biodiversity loss (1–3) and will likely interact in complex ways to further threaten native species (4). Invasive species often have higher tolerances to changing environmental conditions than native species (5) and may be favored as climate change proceeds (6, 7). Thus, many populations of native species may need to cope with both altered abiotic conditions and biotic interactions under future climate change or become extirpated (8, 9). Freshwater ecosystems are experiencing an outsized loss of biodiversity (10–12) and are particularly vulnerable to the combined effects of climate change and invasive species (6, 13). Despite these concerns, few empirical studies have examined the joint impacts of changing abiotic conditions and interactions with invasive species on native freshwater species across broad spatial and temporal scales (14).

Trout—a group of cold-water fishes of enormous ecological and socioeconomic value (15)—are excellent organisms for examining these critical threats to freshwater ecosystems. Like many freshwater species, the distribution, abundance, and phenology of trout are strongly influenced by climatic conditions through species-specific adaptations to water temperature and flow regimes (16, 17), and climate-induced changes in these environmental conditions are predicted to have detrimental effects on many trout populations (17, 18). Moreover, invasive trout species have been widely introduced for recreational fisheries (19) and can affect native trout through competition, predation, and hybridization (16, 20). Increasing evidence suggests that climate change may be facilitating expansion of invasive trout, potentially to the detriment of native trout species (17, 21, 22). However, how climate-induced changes in

temperature and stream flow interact with invasive species to influence the distribution of native trout across space and through time remains a critical uncertainty for developing effective climate adaptation strategies.

In this study, we use long-term monitoring data to examine how the distributions of native bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; here referred to as cutthroat trout) have been influenced by climate change and invasive trout species across the northern Rocky Mountains of Montana, USA. This region is well suited to examine these dynamics because it is a stronghold for native trout and spans diverse environmental gradients. Invasive trout species, including brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*), have been widely introduced for sportfishing from the late 1800s to the early 1970s (19). Moreover, the region has warmed at nearly twice the rate of the global average over the past century (23), resulting in rising stream temperatures, reductions in summer flow, and increased winter flooding (24–27). Previous distribution modeling using space for time substitution projected a 47% decline in total suitable habitat for native and invasive trout species across the interior western United States (17). However, time-series analyses conducted on smaller spatial scales in the northern Rocky Mountains show that warming temperatures may benefit some invasive trout species (28, 29). We hypothesized that an increase in the distribution of invasive trout could further imperil native trout species beyond the direct challenges posed by shifting climatic conditions.

To test this hypothesis, we assessed the effects of rising stream temperatures and changing hydrological conditions on the distributions of five interacting trout species (native cutthroat trout and bull trout, and invasive brook trout, brown trout, and rainbow trout) using a multispecies dynamic occupancy model (30, 31). Dynamic occupancy models allow the direct modeling of local colonization and extinction processes, which leads to a more accurate characterization of environmental niches and interspecific interactions (31, 32). We parameterized this model with 21,917 fish

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surveys collected over 30 years (1989–2018; Fig. 1). We modeled initial occupancy (1989–1993) and subsequent annual colonization and persistence probabilities (1994–2018) as functions of the presence of invasive species and high-resolution (1 km) estimates of summer stream temperature (33), summer flow (34), and winter flood frequency (34) (fig. S1). We then used parameter estimates from the dynamic occupancy model and climate change projections under the A1B emissions scenario (33, 34) [similar to the Representative Concentration Pathway (RCP) 6.0 emissions scenario] to predict the distribution of all five species across the entire stream network (127,705 km) annually from 1993 to 2080. Species interactions were allowed to evolve in our model because the distributions of invasive species could shift with climate change. Last, we conducted a sensitivity analysis to identify the main drivers of the distribution shifts for each species. Together, these analyses describe past and future effects of changing climatic conditions and invasive species on native aquatic biota, thereby providing a detailed examination of how climate change acts directly and indirectly to influence aquatic ecosystems.

RESULTS

Local persistence and colonization probabilities

Differences in local persistence and colonization probabilities revealed distinct environmental niches among trout species (Fig. 2 and table S1). Invasive rainbow trout and brown trout persisted in warmer streams with higher flow, whereas brook trout persisted in streams with cooler temperatures and relatively lower flow (Fig. 2A and B). Native bull trout persisted in colder streams with higher flow (Fig. 2, A and B). In contrast, native cutthroat trout had high persistence probabilities across a wide range of temperature and flow regimes (Fig. 2, A and B, and fig. S2).

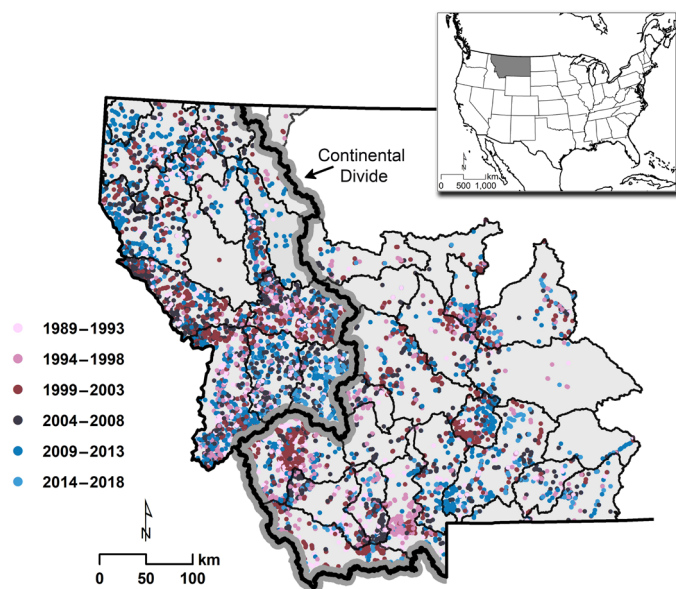


Fig. 1. Fish surveys used to characterize trout distribution shifts in the northern Rocky Mountains of Montana, USA. Fish surveys collected between 1989 and 2018 (21,917 surveys) grouped by 5-year periods. The continental divide separates two major river drainages, the Columbia and Missouri River drainages, which have considerably different environmental conditions.

Native bull trout and cutthroat trout also differed in their responses to invasive species. The presence of brown trout lowered the local persistence of bull trout (Fig. 2C), but this was offset by higher colonization rates (Fig. 2F). This suggests that brown trout cause increased habitat turnover for bull trout rather than complete displacement. In contrast, the presence of invasive species, including brook trout and, especially, rainbow trout, substantially decreased local persistence of cutthroat trout (Fig. 2C).

Both native trout species, as well as brook trout, generally had low colonization probabilities across all environmental conditions (Fig. 2, D and E, and fig. S3). This suggests that once lost, native species (and brook trout) are unlikely to recolonize streams. On the other hand, invasive brown trout and rainbow trout had the highest colonization rates, particularly in streams with moderate to high flow (Fig. 2E), suggesting that the distributions of these species are shifting across the landscape.

Past and future shifts in distribution sizes

We detected region-wide declines in the distribution sizes (i.e., the proportion of occupied stream length) of native trout species in the past and predicted continued declines under future projections (Fig. 3 and table S2). The length of occupied habitat for bull trout and cutthroat trout declined by 18 and 6%, respectively, from 1993 to 2018 (Fig. 3B) and was predicted to decrease by an additional 39 and 16% by 2080 under the A1B emissions scenario. In contrast, changes in the distributions of invasive species varied from contractions to expansions. The distribution of brook trout declined by 16% in the past and was projected to decrease by an additional 15% in the future. Brown trout declined slightly in the past (5%), and the size of their overall distribution was projected to remain stable in the future (2% increase). Conversely, the distribution of rainbow trout expanded in the past (6%) and under future projections (10%). These trends suggest that invasive rainbow trout may become more widely distributed than cutthroat trout by the end of the century in the northern Rocky Mountains (Fig. 3A).

Examination of trends in occupancy among watersheds revealed considerable spatial variation in distribution shifts. All species underwent both declines and expansions in at least some watersheds over the past 25 years (Fig. 4, A to E). However, future projections showed less spatial variability (Fig. 5, A to E), where habitat became consistently less suitable for both native trout species and more suitable for invasive rainbow trout across the majority of watersheds (Fig. 5, A, B, and E). We also found substantial differences in predicted future distribution shifts east and west of the Continental Divide in the Missouri and Columbia River drainages. As of 1993, native trout species were more broadly distributed west of the Continental Divide where abiotic conditions were more hospitable, while all three invasive trout species were more common on the east (figs. S1 and S4). However, future predictions suggest that the distributions of invasive brown trout and rainbow trout will substantially expand west of the Continental Divide (21 and 19%, respectively) but not to the east, while brook trout are predicted to decline less markedly west of the Continental Divide (11%) than east (17%). Overall, the increase in invasive trout and the decline of native trout are occurring more rapidly west of the Continental Divide, the current stronghold for native trout in the region (fig. S4). These results suggest that the more dire environmental conditions in the east may portend future conditions in the west without sufficient conservation action.

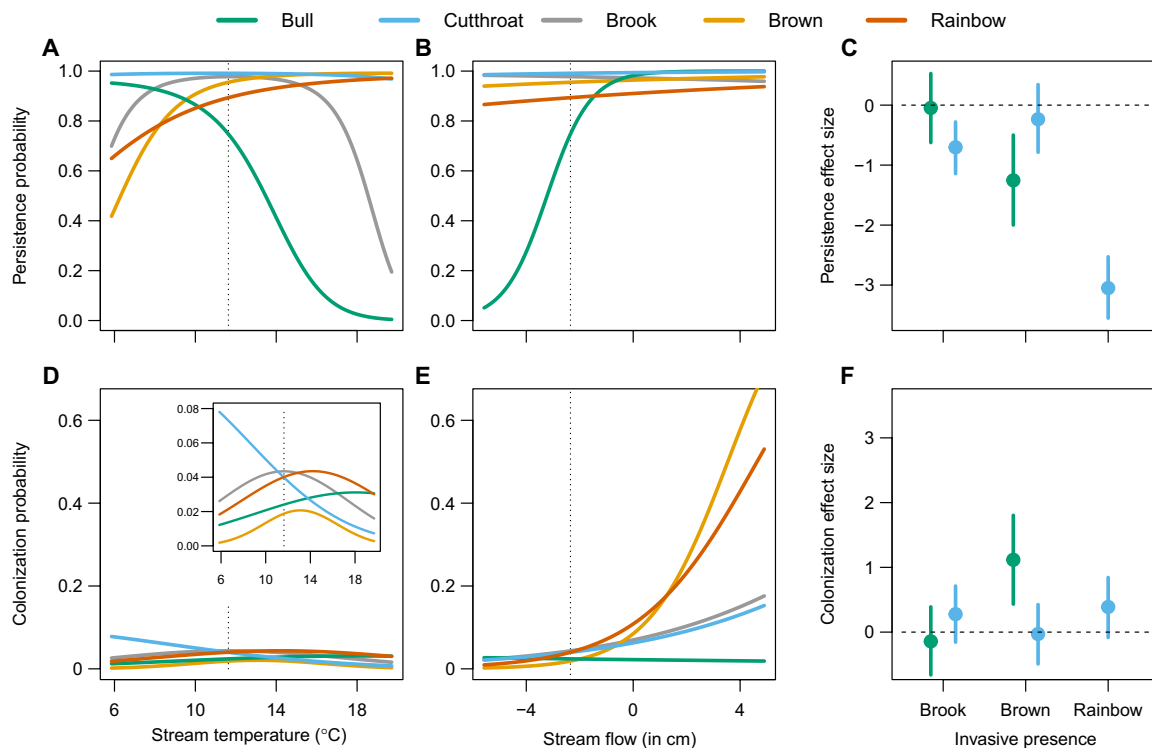


Fig. 2. Abiotic and biotic factors influencing local persistence and colonization probabilities. The effects of summer stream temperature, summer stream flow, and the presence of invasive trout on annual local persistence (A to C) and colonization (D to F) probabilities. The effects of summer stream temperature and summer flow are shown, while all other abiotic covariates are held at their mean and biotic interactions are excluded. Effect sizes of invasive species on native trout persistence (C) and colonization (F) probabilities are shown on the logit scale, with bars representing 95% credible intervals. Black vertical dotted lines represent the mean stream temperature and flow (A, B, D, and E). The inset in (D) shows the same trends with an expanded y axis.

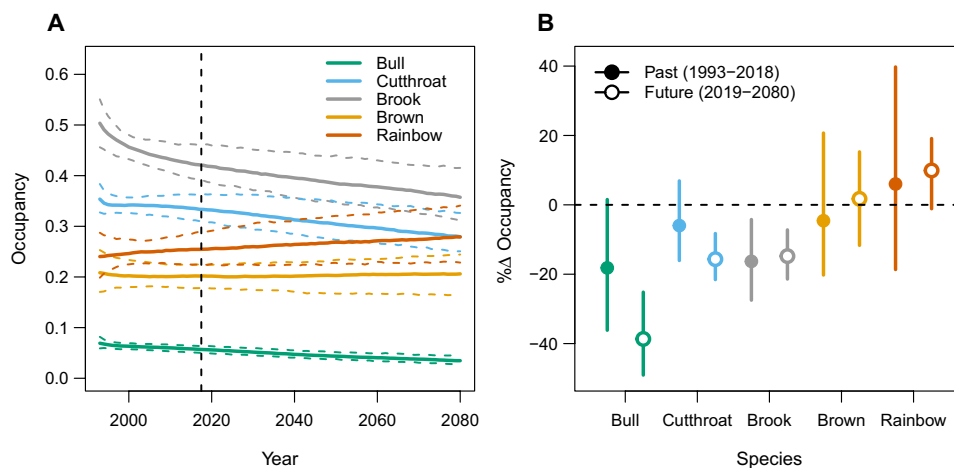


Fig. 3. Past and future trends in the proportion of occupied stream length across the Rocky Mountains of Montana, USA. (A) Trends in the predicted proportion of stream length occupied (i.e., occupancy) from 1993 to 2080. The vertical dashed line indicates the final year of past predictions (2018). (B) Past and future estimated percent changes in occupancy (note that the periods are different lengths). Ninety-five percent credible intervals are indicated by dashed colored lines (A) and solid colored bars (B). Climate change projections assume the A1B emission scenario.

As future climate change projections are inherently uncertain, we also examined the sensitivity of our future projections to the rate of climate change. Specifically, we reestimated future distribution sizes when climate-induced changes in summer stream temperature, summer flow, and winter flood frequency were 50% greater by

2080 than predicted under the A1B emissions scenario, reflecting outcomes under high emissions scenarios (e.g., A2 or RCP 8.5). These more extreme projected changes had little influence on the future distribution sizes of brown trout and rainbow trout, as compared to projections under the A1B emissions scenario (fig. S5). In

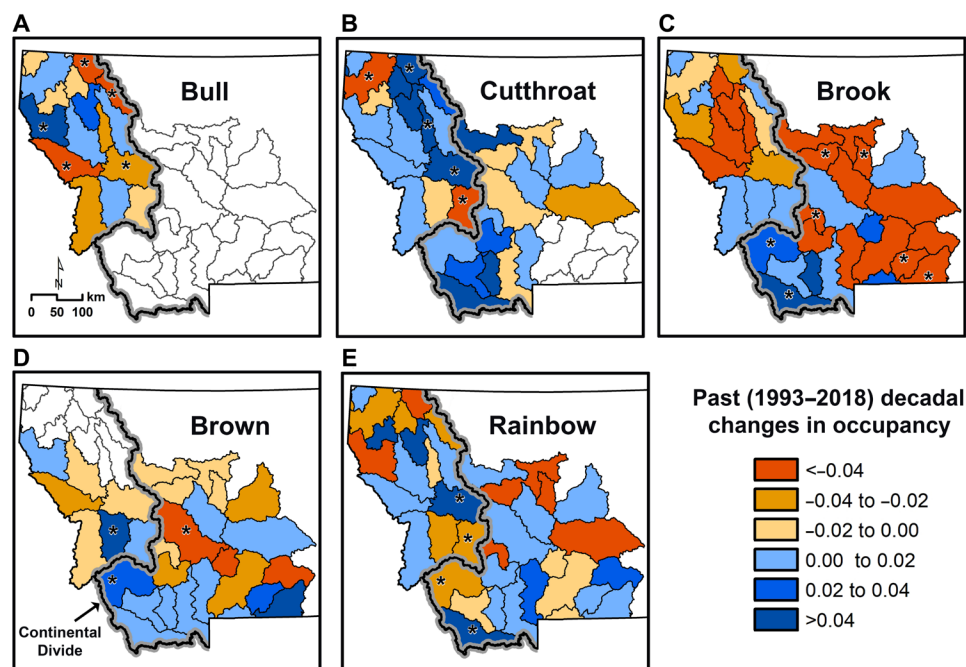


Fig. 4. Spatial variation in past shifts in the proportion of occupied stream length across the Rocky Mountains of Montana, USA. Past (1993–2018) decadal changes in the proportion of occupied stream length by subbasin (HUC 8). Asterisks indicate 95% credible intervals that do not overlap zero.

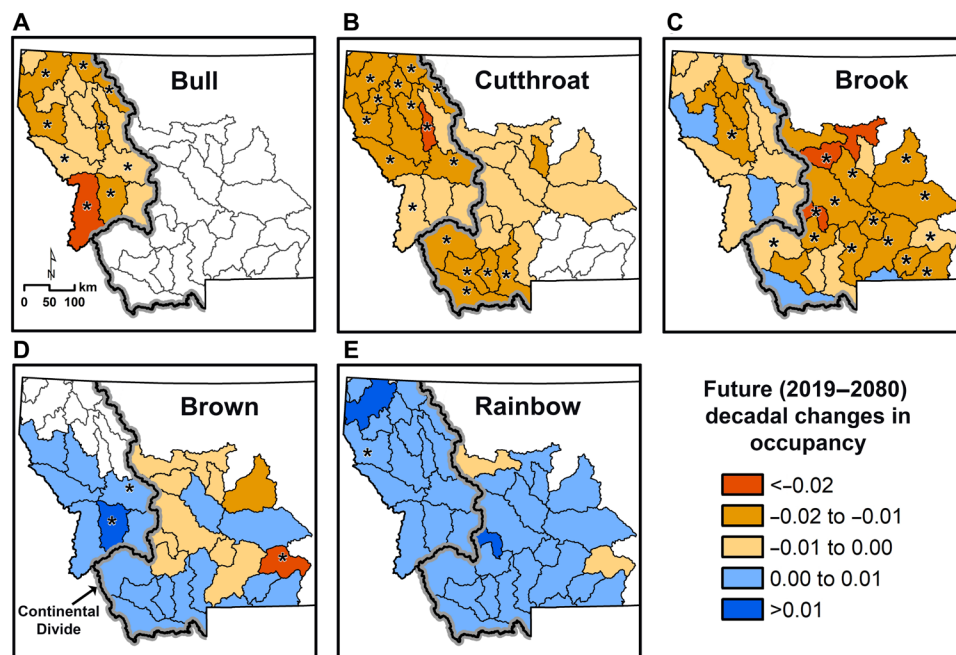


Fig. 5. Spatial variation in predicted future shifts in the proportion of occupied stream length across the Rocky Mountains of Montana, USA. Predicted future (2019–2080) decadal changes in the proportion of occupied stream length by subbasin (HUC 8). Asterisks indicate 95% credible intervals that do not overlap zero.

contrast, both native trout species, as well as brook trout, were predicted to experience greater declines under the more extreme climate change scenario, with the distributions of bull trout and cutthroat trout predicted to decline by 62 and 27%, respectively. These results suggest that the faster climate change proceeds, the more native trout will decline and the more invasive trout will be favored.

Drivers of distribution shifts

Sensitivity analyses in which aspects of global change were omitted from future projections revealed that altered abiotic conditions under climate change likely promoted the stability or expansions of invasive brown trout and rainbow trout (Fig. 6). Without future increases in stream temperature, the distribution size of brown trout

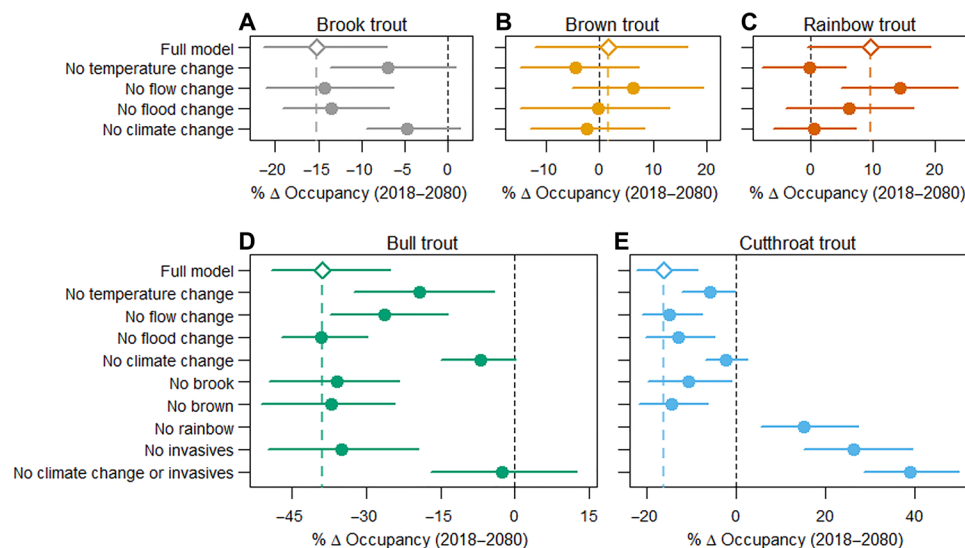


Fig. 6. Sensitivity analysis depicting how omitting aspects of climate change and invasive species presence influences predicted occupancy in 2080. (A to E) Percent change in predicted occupancy from 2018 (based on the full model) to 2080 when an element of global change was omitted. To omit elements of global change, we held abiotic variables constant at their 2018 values and assumed that invasive species were completely absent in the region. In addition to omitting single elements of global change, we also tested the effect of no climate change (i.e., no change in summer flow, winter flood frequency, or summer stream temperature), no invasive species (i.e., all of the invasive species were omitted), and the combination of no climate change and no invasive species. The diamonds and colored dashed lines represent the percent change for the full model (i.e., including climate change and invasive species). Horizontal colored bars are 95% credible intervals. The black dashed lines are included as a reference at no change in occupancy.

was predicted to decline by 4% from 2018 to 2080, rather than remain stable (Fig. 6B), and, similarly, the distribution size of rainbow trout was predicted to remain stable rather than increase (Fig. 6C). Although future reductions in summer flow were predicted to decrease the occupancy of both species, the net effect of changing thermal and hydrological conditions allowed brown trout and rainbow to occupy a greater amount of habitat than if climate change did not occur (Fig. 6, B and C). In contrast, climate change negatively affected brook trout; without increasing summer temperatures, brook trout would have only declined by 4%, less than one-third of the predicted decline in the full model (Fig. 6A).

The factors responsible for distribution declines differed markedly for the two native trout species. The decline in bull trout occupancy was primarily explained by reductions in summer flow and increases in summer stream temperature, not interactions with invasive species (Fig. 6D). Without climate-induced changes in flow and stream temperature, bull trout were predicted to undergo much smaller declines of 26 and 19% by 2080, and without changes in any abiotic conditions, bull trout were predicted to decline by only 7%. Conversely, the future distribution size of bull trout was predicted to be similar with or without invasive species in the region.

In strong contrast to bull trout, invasive species had substantial adverse effects on the future occupancy of cutthroat trout (Fig. 6E). Without invasive species, cutthroat trout were predicted to occupy 26% more habitat in 2080 than in 2018 despite rapid changes in stream temperatures and flow. The removal of rainbow trout alone was predicted to allow cutthroat trout to occupy 15% more habitat in 2080 rather than decline. The climate-induced reduction in suitable habitat was smaller for cutthroat trout than bull trout. Without rising stream temperatures, the distribution size of cutthroat was predicted to undergo a decline of 6%, but this was, at least

in part, due to reduced interactions with invasive species, which are tracking changing abiotic conditions upstream into cutthroat trout habitat (fig. S6). However, cutthroat trout were predicted to occupy the most habitat if no invasive species or climate change occurred, demonstrating the joint impacts of these stressors on future distributions.

DISCUSSION

Interactions between climate change and invasive species are key uncertainties in future projections of biodiversity change (6). Using long-term monitoring data spanning diverse freshwater ecosystems, we show that past and projected future declines of two native trout species were driven by climate-induced reductions of suitable habitat and expansion of invasive species. However, the relative impacts of these threats differed markedly among ecologically similar, co-occurring native species, demonstrating that species-specific climate adaptation strategies may be needed for conservation of freshwater biodiversity.

We found that declines in bull trout distributions were primarily driven by climate-induced increases in water temperatures and decreases in summer flow. These changing abiotic conditions reduced the distribution of bull trout by 18% from 1993 to 2018 and are predicted to cause an additional 39% decline by 2080. Bull trout are habitat specialists that require cold, connected, high-quality, and complex riverine habitats for persistence (35), and the loss of these critical habitats due to climate change has contributed to their decline (36–38). In contrast, declines in cutthroat trout were primarily driven by negative interactions with invasive brook trout and, especially, rainbow trout. Brook trout can outcompete cutthroat trout (39), while climate-induced expansions of rainbow trout lead

to hybridization and genomic extinction of cutthroat trout (28, 40). Unexpectedly, in the absence of invasive species, our projections suggest that cutthroat trout could occupy more habitat at the end of the century than at present despite rapid climate change, consistent with a recent physiological study that found that cutthroat trout have a higher thermal tolerance than previously documented (41).

The distinctive pathways by which climate change threatens native trout species highlight the need for different management and climate adaptation strategies. For example, conservation efforts for cutthroat trout may be better aimed at reducing invasive species through intensive suppression and eradication efforts (42, 43) and intentional isolation of at-risk populations (44). Conversely, conservation efforts for bull trout could focus on protecting, reconnecting, and restoring critical cold-water habitats across entire riverscapes (35, 45). However, the scope for mitigating climate impacts on bull trout may be more limited because an increasing amount of stream habitat—much of which is in protected areas with minimal human impact (46)—is predicted to exceed their narrow thermal niche as the climate continues to warm. Accounting for species-specific sensitivities to climate change and its interactions with other stressors, such as with invasive species, is a prerequisite for effective climate adaptation planning that could extend beyond freshwater fishes to include a range of other taxa.

Species distribution models are increasingly used to make projections of species' responses to future climate change, but efforts to validate these results with past data are rare (16). Our results provide empirical evidence that climate change has already had strong ecological impacts on native trout across the northern Rocky Mountains. Smaller-scale studies on occupancy and population dynamics within the region have documented climate-associated declines in native trout (29, 36–38) and increases in invasive brown trout and rainbow trout over time (28, 29, 40). We show that these trends have also occurred across a broad and ecologically diverse region, but with considerable spatial variation in occupancy shifts. Although native species distributions increased in some watersheds over the past 25 years, our future projections show region-wide declines through 2080. As status quo management is implicit in our model, this suggests that climate change impacts may soon overwhelm current conservation strategies unless more proactive and innovative measures are implemented.

Several previous bioclimatic studies have projected substantial declines in both native and invasive trout distributions (17, 21, 47). For example, another broad-scale study in the interior western United States (which encompasses our study region) projected marked declines in both native cutthroat trout (58%) and invasive brook trout (77%), brown trout (48%), and rainbow trout (35%) by 2080 under the A1B emissions scenario. In contrast, we predict smaller declines in cutthroat trout (16%) and brook trout (15%) and increases in the distributions of invasive brown trout (2%) and rainbow trout (10%), with more pronounced increases west of the Continental Divide (21 and 19%, respectively). The disparity between these findings could be due to several factors. First, ecological conditions in the broader region examined in (17) could differ from those in the northern Rocky Mountains, which contains a substantial amount of protected cold-water habitats. Second, the previous analysis used air temperature as a surrogate for stream temperature to estimate changes in thermally suitable habitat (17), which may have overestimated the amount of future habitat losses. The latter possibility emphasizes that species range projections, including

those here, should be adaptively updated as downscaled climate models are developed and future climate change simulations are updated. Last, our use of an extensive temporal dataset in a multi-species dynamic occupancy modeling framework likely improves future predictions of species distributions compared to models based on a single time period (48). Occupancy models that use space-for-time substitution assume that species are in equilibrium with the environment, which is unrealistic for species experiencing range shifts (32). This highlights the importance of broad-scale and long-term datasets for understanding the effects of climate change and other anthropogenic stressors on freshwater biodiversity.

A major strength of our modeling approach was our ability to account for interactions among multiple native and invasive trout species under changing climatic conditions. However, other invasive fishes that we did not consider may pose additional threats to native trout persistence. For example, invasive lake trout (*Salvelinus namaycush*) have caused declines in bull trout and cutthroat trout populations inhabiting lake ecosystems (38), emphasizing that invasive species negatively influence bull trout in some habitats. Looking forward, smallmouth bass (*Micropterus dolomieu*) have been expanding and affecting native salmonids (*Salmonidae*) in some rivers, a pattern that is predicted to continue under future climate change (49, 50). While our model may partially account for these additional interactions via watershed-level random effects, more research is needed to understand how climate change will affect the community structure of entire aquatic ecosystems for climate adaptation planning and mitigation.

Our results add to a growing body of evidence that climate change threatens freshwater biodiversity by altering both abiotic conditions (51) and biotic interactions (9). Globally, over one-third of freshwater fishes are predicted to be threatened by future climate-induced changes in water temperature and flow in at least half of their range (52). Compounding this threat, many invasive species may be “poised to prosper” and outperform native species in aquatic ecosystems under future climate change (6), thereby further homogenizing freshwater biodiversity (7, 53). We add to this body of research by demonstrating that the relative threats of direct and indirect climate impacts can differ substantially for ecologically and phylogenetically similar native species. Progressive climate adaptation strategies will be essential to reverse declines in native species and prevent further homogenization of freshwater ecosystems in the face of rapid environmental change.

METHODS

Study region and delineation of stream segments

Our study area encompasses the Rocky Mountains of Montana, USA. This region is a stronghold for native trout species and spans large thermal and hydrological gradients (fig. S1). We restricted the analysis to streams and rivers with available environmental data. Further, our study did not include lakes or the potential impacts of invasive species and climate change in lake ecosystems. Our study area included 127,705 km of stream in 39 subbasins [Hydrologic Unit Code (HUC) 8]. The study area was primarily within two major river drainages, the Columbia River and Missouri River basins.

We divided the regional stream network into biologically significant stream segments. Stream networks are composed of linear sections of stream that merge with other streams at confluences. These stream confluences are often associated with changes in

environmental conditions (54, 55) and are also natural locations to begin fish surveys. Confluence to confluence stream segments are thus a meaningful spatial scale to study ecological processes (56) while accounting for variation in detection probability.

We used the National Hydrography Dataset to delineate confluence to confluence sections of stream. Stream segments were then created on the basis of several additional criteria. First, we merged stream sections of the same stream order (a metric of stream size based on contributing tributaries) until the length was ≥ 2 km or the stream order changed. Second, as larger streams and rivers are minimally influenced by confluences with smaller streams (54) and survey distance is generally greater in larger streams, we scaled the stream order used to determine the terminus of a stream segment based on the size of the focal stream. The downstream terminus of stream segments in second- to fourth-order streams was their confluences with streams that were one order lower (e.g., a third-order stream segment ends at its confluence with a second-order stream), and the downstream terminus of fifth- and higher-order stream segments was their confluences with streams that were one or two orders lower (e.g., a fifth-order stream ends at its confluence with a third- or fourth-order stream). Third, sections of stream that crossed permanent fish movement barriers such as waterfalls and dams (Montana Fish, Wildlife & Parks MFISH database) were used to break stream segments. Last, we excluded above barrier drainages that only contained a single first-order stream because colonization of these stream segments is impossible, and stream segments less than 50 m were deemed too small and removed from the analysis. This resulted in 39,638 stream segments with a median length of 2.6 km (interquartile range = 2.1 km).

Fish surveys

We used electrofishing data from 1989 to 2018, which covers the years with the most extensive sampling and starts well after the stocking of nonnative trout species ended (see below for stocking details), providing 21,917 surveys (Montana Fish, Wildlife & Parks MFISH database). We included all stream segments with at least one survey in our occupancy model (4633 stream segments covering 21,874 km). We simplified surveys to detections or nondetections for each species. Detections were inferred from any survey in which at least one individual of the focal species was captured, regardless of the life stage. Nondetections were inferred from surveys that failed to detect any fish or detected a salmonid species but not the focal species. False-positive detections were unlikely because visual identification of trout is reliable, except for hybrids between rainbow trout and westslope cutthroat trout. Any fish visually identified as a hybrid between these species was considered a rainbow trout because conservation efforts in Montana prioritize nonhybridized cutthroat trout. Hybrids between brook trout and bull trout are less common but were likewise considered to be brook trout in this analysis.

Covariates

Initial occupancy, colonization, and persistence probability were all modeled as a function of summer stream temperature and flow, which are key limiting factors for all trout species throughout their native and invasive ranges and are often considered “master variables” in freshwater ecology (16, 33, 34). In addition, we included winter flood frequencies in all biological models because fall spawning trout (including bull trout, brook trout, and brown trout) can be

negatively influenced by winter flooding (17). We limited abiotic covariates to these three well-supported factors to avoid oversaturating the model because directly modeling colonization and persistence probability requires a large amount of temporal data. We obtained spatially explicit summer stream temperature predictions from the NorWeST database (33). Mean summer flow and winter flood frequency (number of winter days in the top 5% of annual flows) were acquired from the Western U.S. Stream Flow Metric Dataset (34). These stream temperature and flow metrics were available both during an initial baseline period (1977–2002 and 1993–2011 for flow and temperature, respectively) and in two future periods under the A1B emissions scenario (2040s and 2080s) (33, 34). We predicted annual stream temperature and flow metrics using separate linear regressions for the two available periods: the middle of the initial period (1987 and 2002 for flow and temperature, respectively) to 2040 and 2040 to 2080. Linear regressions were fit separately for each stream segment, and temperature and flow were predicted in each stream segment for every year from 1989 to 2080. Thus, the climatic covariates were both spatially and temporally explicit. We obtained covariates for each stream segment using ArcGIS, and because these covariates had a spatial resolution of 1 km, covariate values were averaged for stream segments greater than 1 km.

Extensive fish stocking records (1924–1980; Montana Fish, Wildlife & Parks MFISH database) were used to estimate a spatially explicit index of stocking intensity for all invasive species. Specifically, stocking intensity was derived for each stream segment using the following equation

$$\text{Stocking intensity} = \sum_i^{\text{\#Locations}} \text{\#Stocked} * e^{-0.05 * \text{Distance}}$$

where # Locations is the number of locations within a connected watershed where stocking has occurred, # Stocked is the total number of fish stocked at a location across all years, 0.05 is the constant decay rate for straying fish, and Distance is the distance to each stocking site in kilometers (40, 57). Stream distances were calculated using the National Hydrography Dataset.

We standardized all continuous covariates (i.e., mean = 0, SD = 1) to improve model convergence. In addition, we transformed stocking intensity, flow, and stream length because these covariates have a strong right skew. Transformations included the cube root of stocking intensity, the natural logarithm of flow, and the square root of stream length. Pairwise correlations of the covariates used in our analysis were all below 0.7 (table S3), suggesting that multicollinearity was not a substantial issue (58).

In addition, stream segments were designated to be impossible to occupy or colonize if they were located in a stream where the focal species has never been detected, either because it is outside of their native range (bull trout never colonized the Missouri River basin) or above a complete stream barrier (Montana Fish, Wildlife & Parks MFISH database). We therefore accounted for habitat fragmentation and its interaction with climate change by not allowing upstream colonization above natural and anthropogenic barriers (59).

Analyses

We used extensive survey data and microclimatic predictions to parameterize a Bayesian multispecies dynamic occupancy model

(31, 60). Dynamic occupancy models account for imperfect detection and directly model local colonization and extinction processes (30, 60). Dynamic occupancy models have closed periods in which multiple surveys are used to model detection probability and open periods in which local colonization and extinction occurs. The open period extended from February 20 to December 14 (298 days) to capture the entire life history of each species, but most surveys (72%) were conducted from July 1 to September 30 (91 days). Further, the range of sampling dates for a given site was much shorter (median = 29 days). Because of the long open period, “occupied” habitat is better interpreted as habitat that is used by the species, rather than habitat that sustains a year-round population.

In a dynamic occupancy model, z_{it} is the latent state representing the true unobserved occupancy of a stream segment i during time t . The occupancy at the first period (z_{i1}) is determined by the initial occupancy probability (ψ_{i1}). For all subsequent time steps, z_{it+1} is conditional on occupancy in the previous time step. Sites that were occupied remain occupied based on the persistence probability (ϕ_{it}), and sites that were vacant become occupied by the colonization probability (γ_{it}). The observed occupancy status for site i at time t during survey j (y_{itj}) is conditional on the latent occupancy status and dependent on the detection probability (p_{itj})

$$z_{i1} \sim \text{Bernoulli}(\psi_{i1})$$

$$z_{it+1} | z_{it} \sim \text{Bernoulli}(z_{it}\phi_{it} + (1 - z_{it})\gamma_{it})$$

$$y_{itj} | z_{it} \sim \text{Bernoulli}(z_{it}p_{itj})$$

Occupancy, colonization, and persistence probabilities were all modeled using generalized linear models with Bernoulli distributions and logit links and using similar sets of covariates because they are influenced by similar processes. We included summer stream temperature, summer flow, and winter flood frequency as covariates in all three of these biological models. Temperature was included as a quadratic in all models because, as ectotherms, trout have a suitable thermal range that dictates where they can occupy, persist, and colonize. Stream length was also included as a covariate in all initial occupancy models because longer stream segments have a higher probability of occupancy, and stocking intensity was included in the initial occupancy models for invasive species.

To account for species interactions, we included the occupancy of invasive species as a covariate in all biological models for native species. Models of native and invasive species were fit simultaneously, allowing the predicted distribution of invasive species in the previous time step to be used as a covariate for native species models while fully accounting for uncertainty in the invasive species distribution. For westslope cutthroat trout, we included the presence of all three invasive species as covariates (20, 40), and for bull trout, we included brown trout and brook trout (38, 61).

We included random effects for subbasin (HUC 8; i.e., mid-sized river drainages) in all biological models, which accounted for spatial autocorrelation and the effects of other environmental processes not directly incorporated in the models. As an example of the model structure, the colonization probability for bull trout in stream segment i at year t (γ_{it}) was modeled as a function of abiotic covariates (temperature_{it}, flow_{it}, and floods_{it}), the presence of

invasive species in the previous year (brook_{it-1} and brown_{it-1}), a random effect for the subbasin using a zero-mean normal distribution with variance σ^2_{HUC} , and an indicator for whether the stream segment was in their possible range (range limit_i; 1 if within the species range and 0 if outside)

$$\begin{aligned} \gamma_{it} = & \text{inverse logit}(\beta_0 + \beta_1 * \text{temperature}_{it} + \\ & \beta_2 * \text{temperature}_{it}^2 + \beta_3 * \text{flow}_{it} + \\ & \beta_4 * \text{floods}_{it} + \beta_5 * \text{brook}_{it-1} + \\ & \beta_6 * \text{brown}_{it-1} + \beta_{\text{HUC},i} * \text{range limit}_i \\ & \beta_{\text{HUC},i} \sim \text{norm}(0, \sigma^2_{\text{HUC}}) \end{aligned}$$

We modeled detection probability as a function of stream order and year (table S4). Although electrofishing has high individual capture probabilities (median = 0.6; fig. S7), accounting for species-level detection probability was necessary because surveys may fail to detect fish when densities are low and when usage varies spatially and by season. We estimated separate intercepts and slopes for four groups of stream orders (1-2, 3-4, 5-6, and 7-8). Stream order likely influences detection probability because alternate electrofishing methods are used in streams of different sizes and fish abundance can vary with stream size. We included a linear effect for the survey year to account for possible temporal changes in detection probability that could bias trends in occupancy (62).

All models were analyzed in a Bayesian framework in the program JAGS (63) called from the programming language R (64) using the rjags and jagsUI packages (65, 66). We used a burn-in of 15,000 iterations, ran 10,000 additional iterations, thinned the chains by 25, and included five chains. We used uniform priors from 0 to 10 for the SDs of the random effects for subbasins. Priors for all covariate parameters were set on the logit scale using a normal distribution with an SD of 1000 and truncated between -5 and 5. These priors typically provided an acceptable range for all parameters, but in the few cases that posterior distributions were visually determined to be constricted, we changed the prior range to -7 to 7 on the logit scale. The priors for the intercepts of detection probability were constrained to be greater than 0.12 (-2 on the logit scale), because values less than this would indicate extremely minimal usage that is of low biological and management interest. In addition, the prior for the quadratic term of stream temperature was constrained to be less than 0 because thermal niches are not U-shaped.

Model convergence and assessment

The model converged well based on visual inspection of Markov chains and \hat{R} values that were less than 1.1 for all estimated parameters (67). To assess the performance of our model, we calculated the area under the receiver operating characteristic curve (AUC), predictive accuracy (i.e., the proportion of correctly assigned detections), and goodness of fit based on posterior predictive checks (31) for all stream segments within the species range limits (table S5 and fig. S8). The goodness-of-fit test suggested that the model fit the data well (Supplementary Text and table S5). AUC values were moderate for brook trout (0.74) and good to excellent for all other trout species (0.83 to 0.92), and predictive accuracy ranged from 0.66 to 0.85. AUC estimates and predictive accuracy were comparable to, and slightly exceeded, those from previous occupancy models in the region (17, 36). When we included all stream segments in the

study area, including those outside of the focal species range limits, AUC (0.78 to 0.95) and predictive accuracy (0.69 to 0.89) increased (table S5).

Past and future occupancy predictions and sensitivity analysis

We used the parameter estimates from the dynamic occupancy model to predict the occupancy of all species in all stream segments within the study region (127,705 km) for each year from 1993 to 2080. Occupancy was calculated separately for 200 Bayesian iterations to incorporate uncertainty in the parameter estimates. We then summarized the spatiotemporal predictions of occupancy in several ways. We calculated the proportion of total stream length occupied for each species separately for each year. This was done for the entire region and also grouped by stream order, subbasin (HUC 8; mid-sized river drainages), and east and west of the Continental Divide in the Missouri and Columbia River drainages (HUC 2; i.e., major river drainages). Although some surveys were available in the Saskatchewan River drainage, we did not separately examine occupancy dynamics in this basin due to the very small sample size. We estimated temporal trends in occupancy by subtracting the 1993 from 2018 predictions to obtain past trends and subtracting 2018 from 2080 predictions to estimate future trends. All of these estimates were calculated separately for each of the 200 iterations to incorporate uncertainty and allow calculation of the mean and 95% credible intervals.

Future projections used the A1B emissions scenario and a mean of 10 global climate models that have the strongest association with key aspects of climate in western United States (Supplementary Text) (17, 33, 68). Although the Coupled Model Intercomparison Project Phase 3 (CMIP3) (including A1B) simulations have now been replaced by CMIP5, CMIP3 and CMIP5 have produced similar ecological projections (69), and A1B is a middle-of-the-road emissions scenario, similar to RCP 6.0. The A1B emissions scenario thus provides a reasonable baseline to examine in future shifts in occupancy. We then conducted a sensitivity analysis to determine how a 50% greater change in abiotic variables by 2080 than under the A1B emissions scenario would influence future occupancy projections, reflecting a high emissions scenario, such as the Special Report on Emissions Scenarios (SRES) A2 and RCP 8.5.

We also conducted additional sensitivity analyses to determine which abiotic and biotic factors were the main drivers of distribution shifts. We reestimated future (2080) occupancy using the parameter estimates from the dynamic occupancy model but while omitting different aspects of global change. To account for climate change, we reestimated future (2080) occupancy while holding one abiotic variable (e.g., stream temperature, summer flow, and winter floods) at its 2018 values. To account for invasive species presence, we reestimated future occupancy while each invasive species was separately removed from the landscape (i.e., the presence was set to 0 for all stream segments and years). We also reestimated occupancy when all climatic variables were held at their 2018 values, all invasive species were omitted, and the combination of both to examine the relative influence of abiotic versus biotic factors on distribution shifts. As with the full model, we used parameter estimates from 200 iterations from JAGS to incorporate uncertainty. We then calculated the percent change in occupancy from 2018 (based on the full model that provides our best estimate of current occupancy) to 2080 for each of the sensitivity models.

SUPPLEMENTARY MATERIALS

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Climate change and expanding invasive species drive widespread declines of native trout in the northern Rocky Mountains, USA

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