Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change

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Broad-scale studies of climate change effects on freshwater species have focused mainly on temperature, ignoring critical drivers such as flow regime and biotic interactions. We use downscaled outputs from general circulation models coupled with a hydrologic model to forecast the effects of altered flows and increased temperatures on four interacting species of trout across the interior western United States (1.01 million km^2), based on empirical statistical models built from fish surveys at 9,890 sites. Projections under the 2080s A1B emissions scenario forecast a mean 47% decline in total suitable habitat for all trout, a group of fishes of major socioeconomic and ecological significance. We project that native cutthroat trout *Oncorhynchus clarkii*, already excluded from much of its potential range by nonnative species, will lose a further 58% of habitat due to an increase in temperatures beyond the species' physiological optima and continued negative biotic interactions. Habitat for nonnative brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* is predicted to decline by 77% and 48%, respectively, driven by increases in temperature and winter flood frequency caused by warmer, rainier winters. Habitat for rainbow trout, *Oncorhynchus mykiss*, is projected to decline the least (35%) because negative temperature effects are partly offset by flow regime shifts that benefit the species. These results illustrate how drivers other than temperature influence species response to climate change. Despite some uncertainty, large declines in trout habitat are likely, but our findings point to opportunities for strategic targeting of mitigation efforts to appropriate stressors and locations.

global change | hydrology | invasive species | niche model | distribution modeling

Nearly all broad-scale analyses of climate effects on freshwater species have focused on temperature shifts, to the exclusion of other climate-driven drivers. Although temperature is a critical determinant of metabolic and physical processes (1), important ecosystem effects on streams and rivers may also be mediated by flow regime and biotic interactions. Flow regime has been described as a "master variable" (2) that controls or influences many aspects of the physical aquatic environment, as well as the timing of reproduction and migration of many organisms (3). Biotic interactions are increasingly recognized as important components of climate-species relationships (4, 5), but are rarely included in projections of species distributions under future climates, with some notable exceptions (6). Competitive interactions in particular are not commonly modeled (but see ref. 7), despite interest in invasive-native species interaction under climate change (8). It is likely that all three factors—temperature, flow regime, and biotic interactions—will play important roles in future aquatic species distributional shifts (8–11).

Trout serve as excellent model organisms for examining how these mechanisms could alter population dynamics and species distributions, for three reasons ("trout" include fishes in the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*). First, although all trout are coldwater specialists, their temperature sensitivities and preferences vary by species (12), implying different responses to warming. Second, trout are also likely to be differentially affected by flow regime changes. Trout are sensitive to high flows after spawning because such flows can scour eggs from gravel nests or wash away newly emerged fry; thus, fall-spawning trout are sensitive to winter floods and spring-spawning trout are sensitive to summer floods (13–15). In some regions, winter floods are projected to increase with warming due to precipitation shifts from snow to a snow-rain mix (16). Third, many native trout populations are threatened by invasions of introduced trout species. For example, brook trout *Salvelinus fontinalis* have displaced brown trout *Salmo trutta* in Scandinavia (17), and brown trout have displaced native trout in North America (18). Strong competitive interactions such as these set the stage for cascading effects of climate change, whereby climate-driven population changes to one species drive population changes in other species (7, 19).

We assessed the effects of temperature, flow regime (particularly flood seasonality), and biotic interactions, as well as topographic and land use variables, on distributions of four trout species: native cutthroat trout *Oncorhynchus clarkii*, and nonnative brook trout, brown trout, and rainbow trout *Oncorhynchus mykiss* (native to 6% of the region and introduced elsewhere). Our domain was the historical range of cutthroat trout in the inland western United States (1.01 million km^2; Fig. 1), where the species is represented by three main lineages (westslope, Lahontan, and Yellowstone groups) and numerous subspecies, all of conservation concern (20). Candidate variables predicting the distribution of each species under current conditions were tested using multilevel generalized linear models parameterized with fish surveys from 9,890 sites. We used multimodel averaging to combine well supported alternative models into a composite model for each species (21). We then forecasted species suitable habitat under climate change using estimated future temperature and flow

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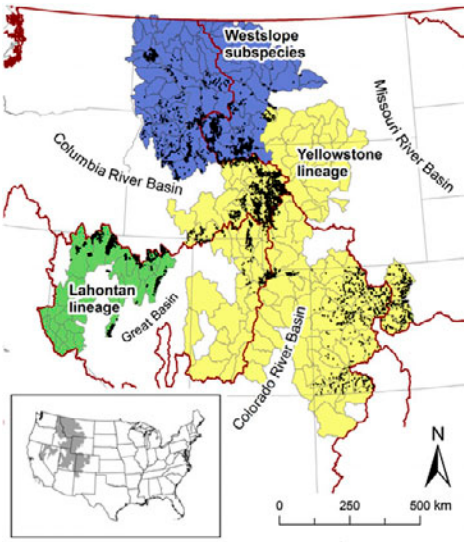

Fig. 1. Study domain and fish collection sites (black dots; $n = 9890$). Boundaries of major river basins (and Canadian border) are shown in red; state boundaries in gray. Ranges of the three cutthroat lineages are indicated by colors.

Table 1. Model-averaged parameter estimates (means ±1 SE) for temperature and flow predictor variables in the composite model for each species

Trout	Variable
Cutthroat	
ptemp	−0.59 ± 0.12
ptemp^2	−0.88 ± 0.13
w99	−0.20 ± 0.11
Brook	
ptemp	−0.66 ± 0.12
ptemp^2	−1.20 ± 0.12
w2	−0.98 ± 0.14
Rainbow	
dtemp	−0.32 ± 0.16
dtemp^2	−0.89 ± 0.18
w99	0.58 ± 0.11
Brown	
ptemp	1.90 ± 0.28
ptemp^2	−1.44 ± 0.26
w95	−1.15 ± 0.22

Variable abbreviations (e.g., "ptemp" and "wtemp") are defined in *Methods*. Parameter estimates are weighted averages of multiple individual models. Variables have been standardized by subtracting the mean and dividing by 2 SD.

metrics from general circulation models (GCMs) simulating conditions in the 2040s and 2080s under the A1B emissions scenario (22), accounting for biotic interactions. We bracketed variability in climate warming predictions by using outputs from one GCM that predicted high warming (MIROC3.2), one that predicted low warming (PCM1), and a composite of 10 GCMs (23). Finally, we used a sensitivity analysis to evaluate the relative importance of temperature, flow, and biotic interactions in determining distributional changes of each trout species under future climates.

Results

The four trout species differed substantially in their relationships with temperature, flood seasonality, and presence of other trout. Brook trout and cutthroat trout occurred in the coldest streams, whereas rainbow trout occupied warmer locations, and brown trout the warmest locations (Table 1 and Fig. 2*A*). Fall-spawning brook trout and brown trout showed a strong negative relationship with winter high flow frequency, as predicted; spring-spawning cutthroat displayed a weak negative relationship, and spring-spawning rainbow trout had a positive relationship (Table 1 and Fig. 2*B*). Cutthroat trout showed a negative relationship to the occurrence of all three other species at either the stream reach or subwatershed scale or both, with some variability among cutthroat trout lineages (Table S1). There was no evidence for biotic interactions among the other species. Other variables of importance to trout distributions were stream slope, mean flow (primarily an indicator of landscape position or stream size), road presence, and distance to the nearest unconfined valley bottom (UVBs, landscape features associated with high densities of fall-spawning trout; refs. 24 and 25). In-sample classification accuracy of models was 64–76%. See *SI Text* for additional model details.

Under the climate projections, both native cutthroat trout and nonnative brook trout showed a strong decline in length of suitable habitat (Figs. 3 and 4). Cutthroat trout was projected to decline by 28% in the 2040s composite scenario and 58% in the 2080s scenario; brook trout was projected to lose 44% and 77% of its range, respectively, for these scenarios. Rainbow trout was projected to decrease modestly (13%) in length of suitable habitat in 2040s, with a moderate decrease (35%) in the 2080s (Figs. 3 and 4). Brown trout was projected to decline by 16% in the short term and 48% in the long term (Figs. 3 and 4). There were very large differences between the MIROC3.2 and the PCM1 model projections of suitable habitat. For example, cutthroat trout was projected to decline by 70% under the 2080s MIROC3.2 scenario but only 33% under the 2080s PCM1 scenario (Fig. 3). We projected that the total length of habitat suitable for one or more trout species would decline by ∼47% under the 2080s composite scenario. This was accompanied by a range shift from larger, low-elevation streams to smaller, high-elevation streams, so habitat volume and trout biomass could decline more than is indicated by the change in stream length.

The sensitivity analysis indicated that individual species declines were associated with different variables. A combination of increasing temperature and increasing winter high flow frequency drove the brook trout losses (Table 2), whereas the declines of brown trout (with much higher thermal tolerances) were attributable almost solely to increasing winter high flow frequency. The more modest declines of rainbow trout resulted from negative effects of temperature increases offset by positive effects of increasing winter high flow frequency. The projected cutthroat trout declines were associated most strongly with temperature increases, but additional sensitivity analyses also showed a substantial role of biotic interactions. Under current conditions, we projected that cutthroat trout would occupy 239,000 km of stream if none of the

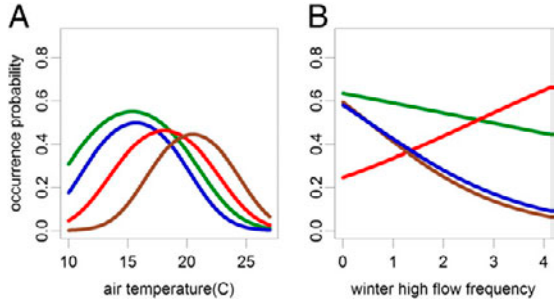

Fig. 2. Occurrence probability of trout species as a function of air temperature (*A*) and winter high flow frequency (*B*). Green indicates cutthroat trout; blue indicates brook trout; red indicates rainbow trout; brown indicates brown trout. The different temperature and flow metrics for different species were standardized to a common *x* axis in each panel to facilitate comparisons; the figures are shown with original axes and with confidence intervals in Fig. S1.

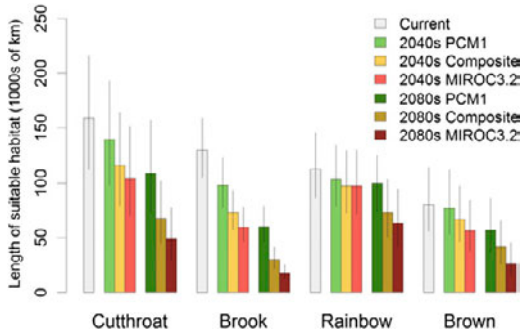

Fig. 3. Projected stream length of suitable habitat for trout under current conditions and climate change scenarios. Whiskers show 90% confidence intervals for projections.

other trout species were present, rather than the 159,000 km, suggesting that nonnative species are responsible for a 33% reduction in cutthroat trout suitable stream length at present (classifying rainbow trout as nonnative). Similarly, under the 2080s composite model scenario we calculated that the length would be 92,000 km instead of 68,000 km, if the other species were absent. Thus, we projected that nonnative species would continue depressing cutthroat trout populations by about 26% in the future.

Discussion

We found that multiple drivers—temperature, flow regime, and biotic interactions—determined the response of trout species to climate change in the western USA. For example, projected declines of one species (brown trout) were driven by increasing frequency of winter high flows, with minimal influence of temperature (except as mediated by flow changes). The projected shift in flow regime also negatively affected brook trout, which like brown trout is a fall-spawning species. However, spring-spawning cutthroat trout and rainbow trout showed a modest negative response and a strong positive response, respectively, to winter high flows. The positive response of rainbow trout likely reflects preadaptation to this flow regime, which is characteristic of much of the species' native range (14). Other researchers have recognized that climate-driven shifts in flow regime will play a role in changes to stream biota and aquatic ecosystems (9, 26), and some have modeled climate-related flow effects on species at the stream scale (27). However, until now this has not been extended to broad scales due to a lack of quantitative estimates of hydrologic metrics under future conditions. Despite the important influence of flow regime, we nevertheless found that temperature increases themselves were likely to play a dominant role in driving future declines of cutthroat trout, brook trout, and rainbow trout. The actual mechanisms for temperature-driven extirpations are likely to be manifold and complex, involving growth rates, incubation times, competitive ability relative to other species, and asynchrony with prey, which can cause negative population growth rates even if temperatures never reach the lethal range for individuals (28).

Biotic interactions were an important driver of native cutthroat trout distributions, which, consistent with past observations, responded negatively to the presence of nonnative trout (24). Both currently and under future climate conditions, the presence of other species reduced the distribution of cutthroat trout by 26–33%, although the species primarily responsible for

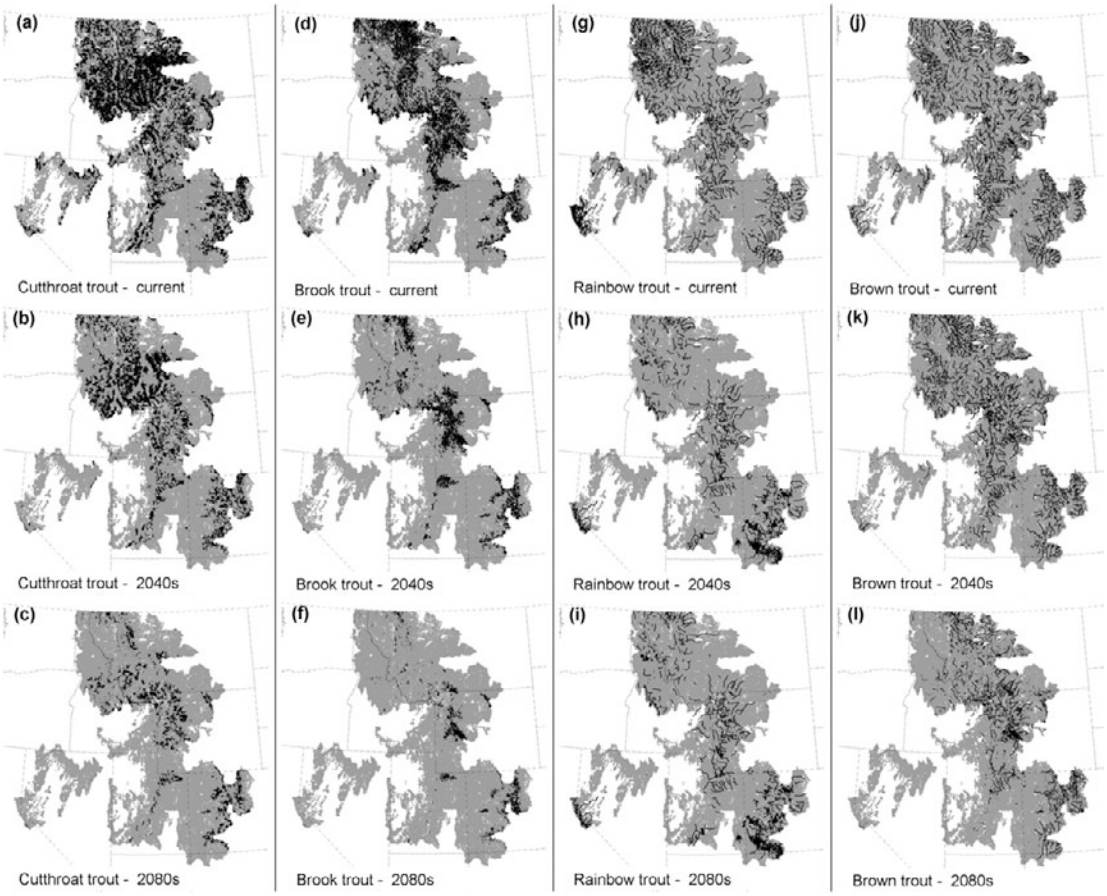

Fig. 4. Projected distribution of suitable habitat for trout under current conditions, 2040s A1B, and 2080s A1B climate change scenarios, based on the composite GCM. Black indicates mostly suitable; gray indicates mostly unsuitable.

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Table 2. Results of sensitivity analysis, indicating importance of climate-related variables in determining suitable habitat for trout under climate change

Condition	Cutthroat	Brook	Rainbow	Brown
Current suitable stream length	159	130	112	80
Projected suitable stream length under 2080s scenario	68	30	73	42
Projected in 2080s if no change in temperature	187 (×2.8)	92 (×3.1)	162 (×2.2)	45 (×1.1)
Projected in 2080s if no change in winter high flows	77 (×1.1)	45 (×1.5)	46 (×.63)	75 (×1.78)
Projected in 2080s if no change in temperature or winter high flows	205 (×3.0)	131 (×4.4)	114 (×1.6)	81 (×1.9)
Projected in 2080s if no change in mean flow	69 (×1.0)	30 (×1.0)	72 (×0.99)	41 (×0.98)

Values indicate projected length of suitable habitat under current conditions (row 1), under projections for the 2080s A1B composite scenario (row 2), and under the 2080s A1B composite scenario with selected climate metrics held constant at current levels (rows 3–6). Units are km × 1,000. Values in parentheses indicate change relative to the 2080s A1B composite scenario (row 2).

this shifted from brook trout to rainbow trout. This adds to the evidence (6, 19, 29) against the argument that biotic interactions are relatively unimportant in determining species distributions at broad scales (30). We did not find evidence of negative interactions among the nonnative species. We had hypothesized that westslope cutthroat trout, with a recent evolutionary history of sympatry with other trout, would have weaker biotic interactions than cutthroat trout lineages that evolved in isolation, but the evidence for this was mixed. Whereas westslope cutthroat trout did show a weaker response to brook trout and rainbow trout, its response to brown trout was stronger than that of the other lineages.

Modeling Notes. We found that the predictive accuracy of our models was only moderate for most species. We attribute this in part to the inconsistent introduction of nonnative species across the study area, to the historical extirpation of cutthroat trout from portions of its range, and to our inability to include fine-scale variables such as fires and debris flows (31) and natural and artificial movement barriers (32), because the data were not consistently available. Consequently, we do not recommend using these models for fine-scale predictions without local validation. In addition, forecasting future distributions is inherently uncertain. Our results indicated that just one source of uncertainty, the choice of GCM, can account for >50% variability in estimates of suitable habitat. Therefore, our results are most useful for understanding the different trajectories and relative climate sensitivities of the different trout species, as well as the habitats that are most sensitive to change (e.g., those where winter flooding will increase along with temperatures), rather than making precise predictions of habitat losses.

Broad-scale species distributional modeling such as this complements results from laboratory studies and finer-scale analyses in advancing our understanding of species niches, because it can describe the full range of actual species relationships to environmental variables. For example, laboratory studies showed that brook trout in Wyoming outcompete cutthroat trout at warmer temperatures (33), but a recent analysis of trout distributions in the interior Columbia River Basin (a subset of the range studied here) indicated that warm temperatures were more limiting for brook trout than cutthroat trout (34). Our results help resolve this apparent contradiction by showing that cutthroat trout have a broader thermal niche than brook trout across the western United States, even though individual cutthroat trout populations could have thermal preferences higher or lower than sympatric brook trout due to local adaptations.

Broader Implications. Our models forecast significant declines in trout habitat across the interior western United States in the 21st century, a result we expect will apply to much of the rest of the temperate world because three of our study species (rainbow, brown, and brook trout) are common on multiple continents. This decline will have significant socioeconomic consequences, as recreational trout fisheries are valued at hundreds of millions of dollars in the United States alone (35). To some extent, warmwater species are likely to replace trout in many streams, providing alternative recreational fishery opportunities, although it is unclear whether common introduced species such as smallmouth bass (*Micropterus dolomieu*) can fully exploit the range of habitats currently occupied by trout. In any case, there will be ecological consequences of a shift in dominant fish species that will affect such things as nutrient cycling and reciprocal terrestrial-stream subsidy balances (36) in ways that are difficult to foresee.

For management agencies charged with maintaining healthy trout populations, global change creates obvious challenges; these are exacerbated by the uncertainty inherent in climate forecasts and the complexity of the climate responses we describe here. We argue that efforts to understand this complexity, in terms of which climatic and biotic drivers are significant for different species in different locations, can point to management actions that are efficiently targeted and robust to uncertainty. For example, there is little that can be done to influence the predicted increase in winter high flows, so some declines in fall-spawning species (e.g., brook trout and brown trout) may be inevitable in regions where flows are likely to shift. In contrast, stream temperature is often influenced by anthropogenic activity and future increases can be offset by restoration measures such as maintenance of stream flows and reforestation (37). Thus, managers interested in conserving cutthroat trout or rainbow trout habitat may wish to focus on such restoration activities, which are likely to provide some benefits regardless of the precise climate trajectory. In selecting actions, managers should consider local conditions; for example, the response of cutthroat trout depends substantially on which nonnative species are present, and this varies from region to region. Overall, we argue that considering biotic interactions and variables other than temperature not only gives us a richer understanding of species-climate relationship, but also can inspire a more strategic portfolio of management alternatives.

Methods

Dataset. The fish occurrence dataset was assembled from fish collections made by state and federal agencies (see *Acknowledgments*) and collectively represented a geographically extensive sample of stream habitats of the interior west of the United States (Fig. 1). As an assembled dataset, it did not have a formal sampling design and was subject to spatial autocorrelation, which was addressed in the analysis as described below. We included only sites sampled using electrofishing ($n = 9{,}522$) or snorkeling ($n = 368$) between 1985 and 2004. Cutthroat trout were detected at 5,055 sites, brook trout were detected at 2,820 sites, rainbow trout were detected at 1,031 sites, and brown trout were detected at 655 sites; 1,437 sites had none of these species. In developing models for the nonnative trout, we used subsets of the database that excluded sites in subbasins (watersheds delineated by 8-digit US Geological Survey hydrologic unit codes; http://water.usgs.gov/GIS/huc.html) where there was no evidence of species introductions. More details are in the *SI Text*.

We selected 12 abiotic variables as candidate predictors of trout species occurrence (see *SI Text*), based in part on an earlier study assessing the relative sensitivities of different trout species to climatic factors in the interior Columbia River Basin (34). We used air temperature as a surrogate for

stream temperature because data for the latter were not widely available. Candidate temperature metrics included a point measurement for the site (ptemp) and the mean temperature in the drainage above a site (dtemp). We calculated four candidate metrics of winter high flow frequency: the probability of the 2-y recurrence interval flow occurring in the winter (w2), the probability of the 1.5-y flow occurring in winter (w1.5), the number of winter days with flows among the top 5% for the year (w95), and the number of winter days with flows among the top 1% (w99). Winter was defined as December 1st through February 28th. Two candidate mean flow metrics were mean annual flow (mflow) and mean summer flow (sflow), with summer defined as the period between the decline of the spring flood and September 30th (38). All flow metrics were derived from the Variable Infiltration Capacity (VIC) model (39) coupled with simple routing (38) to produce daily hydrographs for stream segments in the 1:100 K National Hydrography Database (NHD) Plus dataset (http://www.horizon-systems.com/nhdplus/). Metrics were selected based on performance in a validation study (38). Candidate metrics for UVBs included a binary measure of whether a site was within a UVB (vbpres) and a continuous measure of the distance in kilometers to the nearest UVB (vbdist). Slope was from the NHD Plus dataset. We used the occurrence of roads within 1 km of the stream segment on which the site was located (road) as a binary land use variable. Roads were from the 2000 TIGER/Line road database (www.census.gov/geo/www/tiger).

The presence/absence data for nonnative species were tested as biotic predictor variables affecting presence/absence of other species. Cutthroat trout, which is not known to displace other trout species in the region, was not considered as a candidate biotic predictor. These biotic predictors were calculated at two scales: (*i*) the site and (*ii*) the subwatershed (12-digit US Geological Survey hydrologic unit code). The latter indicated whether there was one or more records of a species occurrence within the drainage. We also tested the hypothesis that westslope cutthroat trout was less affected by nonnative trout than the other cutthroat trout lineages by including an interaction term.

Model Building. We used multilevel logistic regression to fit species distribution models for the four trout species. This method allowed us to specify potential relationships between candidate variables and species occurrences based on a priori hypotheses (*SI Text*; ref. 34), and to address spatial autocorrelation. Multilevel modeling reduces parameter bias associated with autocorrelation by modeling errors at multiple levels (40) and is well suited to the hierarchical structure of stream networks (41). We specified a multilevel model with groups at the subbasin level.

Our first step was to identify the best-supported metric from each group of correlated metrics of the same type (for example, ptemp and dtemp for temperature) for each species. For select variables (ptemp, dtemp, mflow, sflow, and vbdist), we tested both a linear and a quadratic effect; for example, mflow was tested by itself and as mflow plus $mflow^2$. The highly skewed mflow and sflow variables were natural-log-transformed to improve model fit; preliminary tests showed no improvements from transforming other variables. Continuous predictor variables were standardized by subtracting the mean and dividing by 2 SD. Each competing model was fit using the glmer function in the lme4 package (42) using R 2.11 software (43). We used Akaike's Information Criterion (AIC) to identify the best metric from each group.

We used these predictors to construct a global model for each species. We fit the global model and all possible subsets using multilevel logistic regression. We ranked the resulting models for each species by AIC and retained all models within 6 points of the best overall model (i.e., AIC_{min}) as a confidence set of parsimonious models (21), excluding those that were the same as a better-ranked model except for the addition of an uninformative parameter (i.e., one that improved the AIC score < 2; refs. 21 and 44). We constructed a composite model for each species using model averaging of this confidence set (21). We calculated the within-sample predictive performance of each composite model, using the area under the curve of the receiver-operator characteristic plot (AUC) and classification accuracy as performance metrics. Then we divided the data into five regions based on latitudinal bands and conducted fivefold cross-validation by withholding data from one region at a time, fitting the model with data from the other regions, and predicting occurrence probabilities for sites in the withheld region. By making projections for distinct geographical regions, each with different combinations of climatic and physical conditions, we hoped to gain insight into each model's performance under future, unobserved combinations of climatic and physical conditions. This was an estimate of model transferability (45, 46).

Projections. We used the composite models to predict occurrence of each species throughout the NHD Plus stream network, excluding lakes and rivers larger than ~2500 km^2 drainage area (ref. 38; *SI Text*), under current conditions and climate scenarios for the 2040s and 2080s associated with the A1B greenhouse gas emissions trajectory (22). The A1B is a middle-of-the road scenario in terms of assumptions for accumulation of greenhouse gases (22). For each of the future time periods, we used projections from three models: (*i*) MIROC 3.2, which projects greater warming and less summer precipitation in the study region than other GCMs; (*ii*) PCM1, which projects less warming and more summer precipitation; and (*iii*) a mean of the 10 IPCC models with the lowest bias in simulating observed climate across the region (23). This resulted in six future scenarios, three for the 2040s and three for the 2080s. The MIROC3.2 and PCM1 models bracketed the range of possible future temperatures; the former projected a mean increase of 5.51 °C in mean summer temperature by the 2080s, whereas the latter projected a mean increase of 2.49 °C for the same period. The GCM model simulations were downscaled using a spatially explicit delta method (23). For each of the scenarios, we used the VIC model to generate hydrographs, from which we extracted the flow metrics described previously. We derived temperature metrics from the downscaled GCM projections. Because biotic predictors were only supported for cutthroat trout, we incorporated biotic data into projections by first modeling other species, and then using the projected biotic data in the forecasts for cutthroat trout (29). For each species, we set the predicted probability threshold to define presence equal to species prevalence in the fitting dataset (47). We mapped the predicted distributions, which we interpreted as suitable habitat, and calculated the total suitable stream length for each species under each scenario.

We conducted a sensitivity analysis to determine which variables contributed the most to species distribution changes under future conditions. We reran the projections using the composite scenario for the 2080s, iteratively holding the hydroclimatic variables (temperature, winter high flow frequency, temperature plus winter high flow frequency, and mean flow) unchanged from current conditions, and recorded the resulting change in total stream length of predicted suitable habitat for each species. To assess the role of biotic interactions, we calculated the total length of predicted suitable habitat for cutthroat trout if there were no other species present (i.e., all biotic interaction parameters set to 0), for the current and 2080s composite scenarios.

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Supporting Information

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SI Text

Best Supported Models for Each Species. There were 2–7 plausible models in the confidence set for each species (Table S2) that were averaged to create a composite model (Table S3), from which we drew inferences. As noted in *Results*, we found that species hydroclimatic relationships were generally consistent with hypotheses. We also found that brook trout was more common in and near UVBs, whereas cutthroat trout was most common at an intermediate distance from UVBs and brown trout was most common far from UVBs (Table S3 and Fig. S1). The negative relationship of brown trout to UVBs was inconsistent with our hypothesis. Rainbow trout showed essentially no response to UVBs in the composite model. All species were most common at low slopes, but brown trout had the strongest slope response (Table S3 and Fig. S1). Brook trout tended to be found in the smallest streams, consistent with predictions. Brown trout and rainbow trout were more common in larger streams, and cutthroat trout showed little relationship with stream size except that they were less common in the smallest streams (Table S3 and Fig. S1). All nonnative species showed a modest positive relationship with road presence, consistent with our hypothesis; however, cutthroat trout showed no relationship with road presence, instead of the hypothesized negative response (Table S3).

Model Performance Results. In-sample model performance ranged from fair for brook trout (AUC ~ 0.7) to good for brown trout (AUC > 0.8), with cutthroat and rainbow trout intermediate (Table S4). Classification accuracy (i.e., the proportion of true presences and absences that were correctly predicted) ranged from 64% to 76%. The cross-validated (transferability) performance was lower for all models, as expected, but the difference was small (≤5% absolute difference in classification accuracy).

Much of the model error was at broader scales and reflected the fact that nonnative trout were patchily introduced across the study area and native cutthroat trout had been extirpated from some regions due to past anthropogenic activities. In an effort to improve error rates, we tested alternative model analysis methodologies (neural networks, Random Forests) but found that although they had superior in-sample classification accuracy they suffered from inferior transferability, and therefore might not yield reliable forecasts. Thus, we concluded that our modeling approach best captured the general relationships between predictor variables and species presence/absence. It is also worth noting that as conditions become more extreme (e.g., as temperatures increase well beyond a species' optimum) predictions become more certain. For example, despite the fact that brook trout model performance is only fair under current conditions, the confidence interval for suitable habitat in the 2080s is relatively narrow because so few locations are even potentially suitable. This is because many streams shift from predicted 30–40% occupancy (interpretable as a prediction of absence with an error rate of 30–40%) to predicted 10–20% occupancy (still a prediction of absence, but with an error rate of 10–20%).

Additional Fish Collection Dataset Notes. Because detection by snorkeling can be less efficient than electrofishing (1), snorkeling sites with fewer than four repeat visits were excluded from the dataset. We also excluded sites with drainage area larger than ~2,500 km^2 because (*i*) our method for estimating flows (2) was not intended for larger basins and (*ii*) detection probabilities for individual species tend to be lower in sites on larger rivers (3). Data from collections on the same stream within 50 m of one another were considered to be from the same location and treated as a single site. Cutthroat trout were detected at 5,055 of the 9,890 sites, brook trout were detected at 2,820 sites, rainbow trout were detected at 1,031 sites, and brown trout were detected at 655 sites; 1,437 sites had none of these species. Historically, cutthroat trout could have been present at any or all of the sites.

Within their respective ranges, all species were considered to be truly absent at sites where they were not detected, even though it is possible that they could have been present but not detected. Although methods exist to incorporate imperfect detection in occupancy modeling (4), doing so in a multilevel modeling framework is complex (5), and we judged it to be of limited benefit for the reasons we explain here. Our dataset consisted of samples collected using multipass electrofishing (one or more surveys) and snorkeling (four or more surveys). Past studies have shown that multipass electrofishing capture efficiency (i.e., chance of detecting a single individual) of the species considered here is ~40–60% (6). This translates to a detection probability of 92–98% if as few as five individual fish are actually present at a site (detection probabilities for four snorkeling visits are comparable). Therefore, in our dataset only sites with very low abundances of fish were likely to be incorrectly labeled as absences, which we contend is reasonable because sites with very few individuals are not likely to represent optimal habitat or persistent populations for that species. A more significant concern is that covariates of interest (e.g., temperature) could be biased because capture efficiencies and occurrence probability respond to the same variables. Using published relationships between capture efficiency and temperature, slope and stream size (3, 6, 7), we calculated that the potential for bias was extremely small, as detection probability would not drop below 90% unless fish abundances were <5 (a possible exception was detection in large rivers, which was why we excluded such locations). Otherwise, the principal consequence of ignoring incomplete detection is to underestimate the magnitude of covariates (8), which implies only that our hypothesis tests are somewhat conservative.

Explanatory Variables: Methods of Calculation and Hypotheses Underlying Variable Selection. We selected 12 abiotic variables including measures of temperature (2 metrics), winter high flow (4 metrics), proximity to unconfined valley bottoms (2 metrics), mean flow (2 metrics), stream slope, and the presence/absence of roads (Table S5).

In-stream temperature data were not broadly available, so we used air temperature as a surrogate (9–11). For consistency, we used the same air temperature dataset as was used in the VIC modeling (described below); these were gridded data interpolated from National Climatic Data Center Cooperative Observer stations (12). We developed site-specific temperatures based on the site's difference in elevation from the mean elevation for the cell, using a lapse rate of $-6.0\ C \times km^{-1}$ (10). We calculated the mean summer temperature for July 15th to August 31st, averaged across the 20 y from October 1977 through September 1997 (i.e., slightly preceding or contemporaneous with fish collection data), abbreviated ptemp; we also calculated the mean temperature in the drainage above the point (dtemp). We hypothesized that all trout species would have a unimodal response to temperature; that is, they would not be found in sites that were too hot or too cold. Based on previous studies, we hypothesized that brook trout and cutthroat trout would tend to be found at colder temperatures than rainbow trout and brown trout (13–15).

We derived estimates of winter high flow frequency from the VIC simulations run for the Great Basin and the Columbia, Colorado, and Upper Missouri river basins (12). Simulations on a daily time step from 1915 through 2006 were performed at 1/16th-degree spatial resolution (~5 km), except in the Great Basin where simulations were performed at 1/8th-degree spatial resolution. We routed simulated runoff and base flow using a simple approach (2) to produce daily hydrographs for stream segments in the 1:100K National Hydrography Database (NHD) Plus dataset (http://www.horizon-systems.com/nhdplus/). From these hydrographs, we calculated four metrics: w2, w1.5, w99, and w95. The first two measured the probability of a 2-y or 1.5-y recurrence interval flow event (respectively) during the winter. Flows of this magnitude are sufficiently large to mobilize bed material, potentially damaging redds and crushing embryos or alevins (16, 17). The latter two metrics, w99 and w95, were the number of days during winter that were among the highest 1% and 5% (respectively) of flows for the year. These were assumed to be flows with velocity sufficient to displace and kill newly emerged fry (18), but not necessarily destroy embryos in redds. Winter was considered to be December 1st through February 28th, and metrics were averaged across the same 20-y period as temperature metrics. Although winter weather can extend well beyond February for much of the region, we used an early cutoff to ensure we excluded the beginning of the spring flood in all areas. We hypothesized that fall spawning trout species (brook trout and brown trout) would display a negative response to winter high flows, but spring spawning species (rainbow trout and cutthroat trout) would not (18–21).

Unconfined valley bottoms (UVBs) are locations where the path of the stream is not laterally constrained by rock (as it is in canyons), and generally characterized by low slope, wetlands, and in some cases glacial deposits. We included two metrics of UVBs: a binary classification of whether a site was within a UVB (vbpres) and a measure of distance in kilometers to the nearest UVB (vbdist). Unconfined valley bottoms were delineated according to an algorithm that identified relatively flat areas adjacent to streams (22), using 30-m digital elevation models. Because UVBs appear to be preferred spawning and rearing locations for fall-spawning trout species, possibly due to groundwater connectivity or moderated winter high flows (23–26), we hypothesized that fall-spawning species would be more frequently encountered in and near UVBs, whereas spring-spawning species would not.

Stream slope values were from the NHDPlus dataset and were derived for stream segments from 30-m DEMs. We hypothesized that all trout species would show a negative relationship with increasing stream slope, possibly because of high frequency of dispersal barriers or unfavorable physical characteristics such as high velocities (23, 27, 28).

For mean stream flow we considered two metrics: mean annual flow (mflow) and mean summer flow (sflow), both derived from the VIC-modeled flow dataset described previously. Mean annual flow was the mean daily flow, averaged across the full year, and then averaged across the same 20-y period used for temperature metrics. The sflow variable was the same but calculated only for the summer, which was defined as the period between the decline of the spring flood peak and September 30th; the calculation of the spring flood decline was made independently for each year for each stream segment (2). Mean stream flow primarily served as an index of stream size. We hypothesized that brook trout would tend to occupy smaller streams, based on past studies (23, 29, 30). For other species, we made no specific hypotheses but allowed for the possibility that responses could be unimodal, with lower occurrence probability in streams that were too small and too large.

The road variable was calculated as a value of 1 if the 2000 TIGER/Line road database (www.census.gov/geo/www/tiger) indicated a road within 1 km of the stream segment on which the site was located, and 0 otherwise. We hypothesized that native cutthroat trout were less likely to occur in regions with roads near streams (road; Table 1) because roads may reduce habitat quality and connectivity and facilitate introductions of nonnative species (31, 32). In contrast, we hypothesized that nonnative brook trout would show a positive relationship with roads, due to greater probability of introductions (legal or illegal) of this species in locations accessible by road (33).

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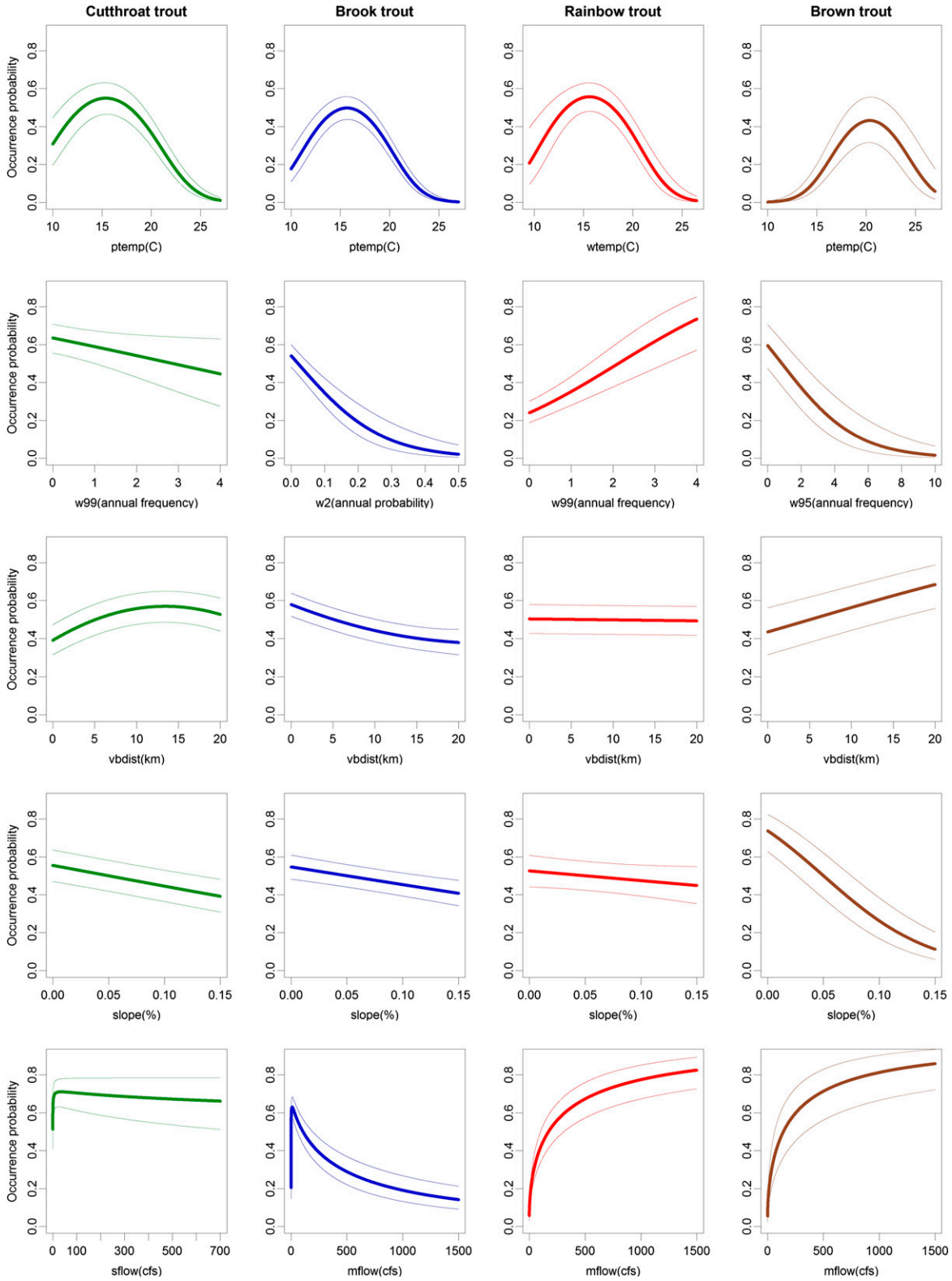

Fig. S1. Occurrence probability of trout species as a function of predictor variables (abbreviations defined in *Methods* and Table S4). Heavy lines indicate mean values; fine lines indicate 90% confidence intervals.

Table S1. Model-averaged parameter estimates for biotic predictor variables in composite cutthroat model

	Parameter estimate for response of cutthroat to					
Cutthroat lineage	Brook	Brook-w	Rainbow	Rainbow-w	Brown	Brown-w
Westslope	−0.30 ± 0.11	−0.45 ± 0.07	−0.35 ± 0.11	−0.32 ± 0.15	−1.38 ± 0.34	NS
Lahontan/Yellowstone	−1.16 ± 0.09	NS	NS	−0.49 ± 0.11	−0.36 ± 0.15	NS

Biotic responses were tested at both the subwatershed scale (variables with the "-w" suffix) and the site scale (no suffix). NS = variable not supported.

Table S2. Differences in AIC (AIC − AIC_{min}) and Akaike weights (w_i) for the confidence set of models for each species

Model	ΔAIC	w_i
Cutthroat trout		
ptemp + $ptemp^2$ + w99 + vbdist + $vbdist^2$ + slope + sflow + $sflow^2$+ brk*west + brkw + rbtw*west + rbt + brn*west	0	0.42
ptemp + $ptemp^2$ + w99 + vbdist + $vbdist^2$ + slope + sflow + $sflow^2$+ brk*west + brkw + rbtw + rbt + brn*west	0.7	0.29
ptemp + $ptemp^2$ + vbdist + $vbdist^2$ + slope + sflow + $sflow^2$+ brk*west + brkw + rbtw*west + rbt + brn*west	3.0	0.09
ptemp + $ptemp^2$ + w99 + vbdist + $vbdist^2$ + slope + sflow + $sflow^2$+ brk*west + brkw + rbtw*west + rbt + bm	3.5	0.07
ptemp + $ptemp^2$ + w99 + vbdist + $vbdist^2$ + slope + sflow + brk*west + brkw + rbtw*west + rbt + brn*west	4.2	0.05
ptemp + $ptemp^2$ + vbdist + $vbdist^2$ + slope + sflow + $sflow^2$+ brk*west + brkw + rbtw + rbt + brn*west	4.3	0.05
ptemp + $ptemp^2$ + w99 + vbdist + $vbdist^2$ + slope + sflow + $sflow^2$+ brk*west + brkw + rbtw + rbt + brn + brnw	5.8	0.02
Brook trout		
ptemp + $ptemp^2$ + w2 + vbdist + $vbdist^2$ + slope + mflow + $mflow^2$ + road	0	0.91
ptemp + $ptemp^2$ + w2 + vbdist + slope + mflow + $mflow^2$ + road	0.6	0.09
Rainbow trout		
wtemp + $wtemp^2$ + w99 + slope + mflow + $mflow^2$ + road	0	0.63
wtemp + $wtemp^2$ + w99 + mflow + $mflow^2$ + road	2.4	0.19
wtemp + $wtemp^2$ + w99 + vbdist + mflow + $mflow^2$ + road	2.5	0.18
Brown trout		
ptemp + $ptemp^2$ + w95 + vbdist+ slope + mflow + $mflow^2$ + road	0	0.61
ptemp + $ptemp^2$ + w95 + vbdist+ slope + mflow + $mflow^2$	1.4	0.31
ptemp + $ptemp^2$ + w95 + vbdist + slope + mflow + road	4.0	0.08

Parameters that differ among models are highlighted in bold. Only candidate models with ΔAIC ≤ 6 are shown.

Table S3. Parameter estimates (means ±1 SE) for all predictor variables in the composite model for each species

Trout	Intercept	Temperature		Winter high flow	Valley bottom distance		Slope	Stream size/flow		Road presence
Cutthroat		ptemp	$ptemp^2$	w99	vbdist	$vbdist^2$	Slope	sflow	$sflow^2$	NS
	1.24 ± 0.20	−0.59 ± 0.12	−0.88 ± 0.13	−0.20 ± 0.11	0.74 ± 0.09	−0.50 ± 0.08	−0.34 ± 0.08	0.41 ± 0.11	−0.21 ± 0.09	
Brook		ptemp	$ptemp^2$	w2	vbdist	$vbdist^2$	Slope	mflow	$mflow^2$	road
	−0.85 ± 0.14	−0.66 ± 0.12	−1.20 ± 0.12	−0.98 ± 0.14	−0.62 ± 0.09	0.18 ± 0.08	−0.29 ± 0.07	0.34 ± 0.09	−0.85 ± 0.09	0.39 ± 0.07
Rainbow		wtemp	$wtemp^2$	w99	vbdist	NS	Slope	mflow	$mflow^2$	road
	−2.14 ± 0.19	−0.32 ± 0.16	−0.89 ± 0.18	0.58 ± 0.11	−0.02 ± 0.14		−0.16 ± 0.16	1.20 ± 0.15	0.33 ± 0.12	0.38 ± 0.11
Brown		ptemp	$ptemp^2$	w95	vbdist	NS	Slope	mflow	$mflow^2$	road
	−2.66 ± 0.30	1.90 ± 0.28	−1.44 ± 0.26	−1.15 ± 0.22	0.58 ± 0.14		−1.62 ± 0.21	1.28 ± 0.19	0.20 ± 0.03	0.20 ± 0.18

Variable abbreviations (e.g., "ptemp" and "wtemp") are defined in Methods and listed in SI Table S4. Variables have been standardized by subtracting the mean and dividing by 2SD. NS = variable not supported.

Table S4. Performance statistics for the top-ranked models for each species

Trout	In-sample AUC	In-sample classification accuracy	Cross-validated AUC	Cross-validated classification accuracy
Cutthroat	0.758	69%	0.709	65%
Brook	0.680	64%	0.653	61%
Rainbow	0.746	69%	0.659	64%
Brown	0.822	76%	0.786	74%

AUC is the area under the curve of the receiver operator characteristic plot. Cross-validated values were calculated with sites assigned to five geographically distinct units.

Table S5. Metrics used as abiotic predictor variables in multilevel logistic regression models of species occurrences. Range and mean are from the model-building dataset

Group	Metric	Abbreviation	Units	Range	Mean
Temperature	Mean summer air temp. at site	ptemp	C	9.8–27.3	17.1
	Mean summer air temp. in drainage	dtemp	C	9.5–26.7	16.4
Winter High Flow	Winter high flow (2 y flow)	w2	Probability	0–3.6	0.12
	Winter high flow (1.5 y flow)	w1.5	Probability	0–13.3	0.36
	Winter high flow (99% annual flow)	w99	Frequency	0–4.5	0.28
	Winter high flow (95% annual flow	w95	Frequency	0–9.65	0.85
Mean Flow	Mean annual flow	mflow	ft^3*s^{-1}	0–2233	25.8
	Mean summer flow	sflow	ft^3*s^{-1}	0–923	9.57
UVB	UVB (binary)	vbpres	—	0/1	0.22
	UVB distance	vbdist	km	0–31	5.11
Slope	Stream slope	slope	—	0–0.53	0.05
Road	Road presence (binary)	road	—	0/1	0.71