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Strong but heterogeneous distributional responses to climate change are projected for temperate and semi-arid stream vertebrates

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Abstract

1. Globally, freshwater systems are threatened by climate change, so projections under various climate change scenarios are needed to inform efforts to protect and conserve already vulnerable taxa.
2. Here, the change in distribution of stream vertebrates was investigated under different greenhouse gas emission scenarios. Using occurrence data from multiple stream surveys in Washington State spanning 559 sites and 24 years, species distribution models for 23 aquatic vertebrate taxa (21 fish and two amphibians) were developed.
3. Models projected changes in taxon distributions for 2070 under representative concentration pathways (RCPs) ranging from 2.6 to 8.5 W m^{-2}. To assess potential biological impacts of these predictions, changes in taxon richness and beta diversity of stream vertebrates were also investigated. Moreover, predictor variables were examined to assess which ones were more important in determining taxon distributions.
4. Substantial changes in the spatial distribution of stream vertebrates were projected for all RCP scenarios by 2070, but the greatest changes were expected to occur under RCP 6.0 and 8.5. The taxa evaluated were predicted to experience substantial increase, decrease, or shift in distribution.
5. Taxon richness of stream vertebrates was forecasted to increase with RCP scenario relative to historical conditions, suggesting that distributional expansions outpaced distributional contractions. However, beta diversity was predicted to decrease considerably, suggesting increased biotic homogenization. Variables important for determining future distributions varied by taxa, with most species influenced by a combination of variables.
6. These results indicate that failing to reduce greenhouse gas emissions will lead to dramatic impacts on stream vertebrates. The magnitude of predicted future impacts was dependent upon RCP scenario, so advancements in policy to reduce carbon emissions are necessary. We also recommend as potential conservation measures preserving cold-water refugia and increasing efforts to lower stream water temperatures by, for example, expanding the riparian cover and/or linking surface water to groundwater.

KEYWORDS
beta diversity, climate change, representative concentration pathways, species distribution models, stream vertebrate conservation, taxon richness

1 | INTRODUCTION

Some of the greatest challenges facing ecologists and conservation biologists today are to better understand and predict the impacts of climate change on biodiversity and to design appropriate conservation programmes to protect it. Many species are expected to experience alterations to their historical distributions in response to climate change, which will ultimately affect local and regional biodiversity (Walther et al., 2002; Pound, Larson & Passy, 2021). For example, studies in Europe have reported distributional changes for a variety of organisms, which have migrated poleward or in elevation (Hickling et al., 2006; Lenoir et al., 2008; Comte & Grenouillet, 2013; Maire et al., 2019). In North America, some birds and cool-water fish taxa have experienced poleward expansion (Babaluk et al., 2000; La Sorte & Thompson, 2007; Alofs, Jackson & Lester, 2014), whereas range contraction has been reported for bull trout populations (Eby et al., 2014). Terrestrial insects are expected to face a range of outcomes, with taxa near the tropics predicted to suffer the most deleterious impacts as they have narrower thermal tolerances than taxa from higher latitudes do (Deutsch et al., 2008). Thus, the expected outcomes of climate change are likely to be species dependent and quite varied. The effects of climate change are further projected to transcend individual species and cause a decline in species turnover (i.e. beta diversity), known as biotic homogenization, as shown for fish, insect, and diatom metacommunities in the conterminous USA (Pound, Larson & Passy, 2021).

Freshwater systems are some of the most threatened ecosystems worldwide (Tickner et al., 2020). By virtue of their relative rarity, streams and rivers, which cover less than 1% of Earth's surface (Allen & Pavelsky, 2018), are at significant risk of biodiversity loss from many different human stressors (Tickner et al., 2020; Su et al., 2021), and declines in freshwater populations continue to outpace those in marine or terrestrial systems (Reid et al., 2019). Global freshwater fish biodiversity has been especially affected, with temperate systems having already experienced some of the greatest biodiversity loss (Su et al., 2021). Therefore, developing reliable forecasts of species distributions in freshwater streams and rivers in the face of different climate scenarios can provide important insights into how to better protect and conserve already vulnerable taxa. Climate influences species distributions, often through species-specific physiological thresholds of temperature and precipitation (Walther et al., 2002). Even small changes in temperature can affect growth, reproduction, and survival, with long-term repercussions (Brown et al., 2004; Waldock, Dornelas & Bates, 2018). Climate change will alter global temperatures, and stream water temperatures are predicted to increase considerably (van Vliet et al., 2013; Isaak et al., 2017). Climate change will also influence the distribution and timing of precipitation, with greater precipitation in the form of rain rather than snow during the winter and much drier summers in many temperate and semi-arid latitudes (Elsner et al., 2010; Mantua, Tohver & Hamlet, 2010; Trenberth, 2011). Temperature and precipitation have been shown to influence fish distributions and biodiversity, with temperature thought to be more important (Griffiths, McGonigle & Quinn, 2014). Nevertheless, it is unknown how general this finding is and the extent to which predicted alterations to temperature and precipitation would have impacts on the future distributions of vertebrate taxa under different climate change scenarios.

Efforts have been made to better understand the measures that can be taken to minimize the impacts of increasing temperatures and altered precipitation patterns on streams and rivers. Some of the proactive options available are designation of more river corridors for protection, acquisition, and protection of headwaters, and restoration of land adjacent to rivers (Palmer et al., 2008; Palmer et al., 2009). Other options that increase surface water–groundwater connections and minimize the loss of flow are also available, including enhancing pool formation through inputs of large wood and beaver dams, as well as protection of riparian wetlands. Determining which factors, both climatic (temperature and precipitation) and local, most influence the distribution of stream vertebrate taxa could help inform the development of conservation plans that minimize some of the adverse impacts of climate change on sensitive taxa.

Climate change is also predicted to contribute to increasing taxon richness in many streams (Buisson et al., 2010; Pound, Larson & Passy, 2021). The reason for this trend in US streams is the difference in climate change response between cold-water and warm-water species, whereby the distributional contraction of cold-water species is weaker than the distributional expansion of warm-water species (Pound, Larson & Passy, 2021). A similar trend is expected in many marine systems owing to niche expansion of warm-affinity generalists (Antão et al., 2020). Notably, increased local taxon richness may be associated with biotic homogenization (Baiser et al., 2012; Waldock, Dornelas & Bates, 2018; Pound, Larson & Passy, 2021; Su et al., 2021), which is a serious environmental threat because it may lead to reductions in ecosystem integrity and resilience to disturbance (Epstein et al., 2018).

To describe possible climate futures based on the volume of greenhouse gases emitted in the years to come, representative concentration pathways (RCPs) have been developed (van Vuuren et al., 2011). They can be used to evaluate ecological consequences under different climate scenarios. A mitigation scenario (RCP 2.6) assumes an elimination of anthropogenic carbon dioxide (CO_2) emissions and high reliance on renewable energy sources. Two stabilization scenarios (RCP 4.5 and RCP 6.0) assume moderate oil consumption and CO_2 emissions that eventually decline. An increasing greenhouse gas emission scenario (RCP 8.5) projects heavy dependence on fossil fuels and both CO_2 and methane emissions roughly tripling. In this study, the distributions of various stream vertebrate taxa were modelled to examine how they would change by 2070 under the four RCP scenarios using species distribution models (SDMs). These models relate field observations to a variety of predictor variables (local and climatic), enabling the exploration of relationships between species and their overall environment (Guisan & Thuiller, 2005). They are commonly used to explore how plants and animals are distributed in space and time (Guisan & Thuiller, 2005; Thuiller et al., 2020; Pound, Larson & Passy, 2021).

Washington State has many high mountain streams and lowland rivers that offer a large gradient in temperature and precipitation, providing an ideal place to examine the potential impacts of climate change on stream communities. The three objectives of this study were to (i) evaluate the expected change in future distributions (i.e. 2070) of stream vertebrates in Washington State under different RCP scenarios compared with historical distributions to assess the role of climate change severity, (ii) determine the impacts of projected RCP scenarios on vertebrate taxon richness and beta diversity, predicting an increase in richness and decrease in beta diversity, and (iii) investigate the relative importance of temperature and precipitation in determining spatial distributions of aquatic vertebrate taxa in 2070 in order to provide potential insights for conservation efforts in the state.

2 | METHODS

2.1 | Study sites and datasets

Stream vertebrate data from 559 sites in Washington State were used, combining collections from the Washington State Department of Ecology (ECY) and the US Environmental Protection Agency (EPA) between 1994 and 2018 (Supporting Information Figure S1). Single-pass electrofishing was implemented across studies, where individual taxa were typically identified to genus or species. For sites with multiple samples or multiple years of data, only the most recent samples were used.

2.2 | Species selection

Ninety aquatic vertebrate taxa (fish and amphibians) have been recorded across the study area. To focus on more commonly observed taxa and to reduce errors associated with small sample size (Stockwell & Peterson, 2002), only those found in at least 4% of sites (≥20 sites) were included, leading to 21 fish and two amphibian taxa being investigated in this study. Three of the taxa examined were not identified to species because of the challenges of identifying to that level in the field. For example, the lamprey in this study were probably either Pacific lamprey (*Entosphenus tridentatus*), river lamprey (*Lampetra ayresii*), or western brook lamprey (*Lampetra richardsonii*), but they were identified to family owing to the difficulty of identifying juveniles or ammocoetes to finer taxonomic levels. In addition, individuals from *Ascasphus* were likely to be either coastal tailed frog (*Ascaphus truei*) or Rocky Mountain tailed frog (*Ascaphus montanus*), but because they were juveniles and therefore difficult to identify, they were identified to genus level. Furthermore, *Dicamptodon* specimens were either coastal giant salamander (*Dicamptodon tenebrosus*) or Cope's giant salamander (*Dicamptodon copei*), but they were identified to genus level also because of the difficulty of distinguishing between the two larval forms. For all three taxa, voucher specimens were not collected, which would have allowed closer examinations, owing to their threatened or unknown status.

2.3 | Local environmental and climatic variables (predictors)

Six variables, all with Pearson correlation coefficients ≤0.71, were chosen for predictive models owing to their ability to affect the distributions of stream vertebrates used in this study (plots for individual taxon responses to variables are shown in Supporting Information Figures S2.1–S7.4). Values for each of the model parameters were obtained for all sites by extracting data using a 5 km buffer around geographical coordinates for each site from each of the databases used. Climatic variables were obtained from the WorldClim database (Hijmans et al., 2005) using CMIP5 climate projections from three global climate models (see later this section). The five 'bioclimatic' variables included in this study were (i) annual mean air temperature, (ii) air temperature seasonality ($SD \times 100$), (iii) maximum air temperature of the warmest month, (iv) precipitation of the driest month, and (v) precipitation seasonality (coefficient of variation). These variables were chosen because they represent seasonal variability or environmental extremes, which are likely to exert impacts in temperate and semi-arid regions. Historical (average for years 1960–1990) and future climatic variables for four RCPs (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5 for 2070 (average for years 2061–2080)) came from the IPC5 climate projections from three separate global climate models (NorESM1-M, CCSM4, and MPI-ESM-LR; no RCP 6.0 was available for MPI-ESM-LR). Values from each global climate model were obtained from 2.5′ spatial resolution GeoTiff files.

Slope for each site was obtained from the NorWeST database (Isaak et al., 2017). Slope was included because it can also influence migration. Values for slope did not change between historical and future scenarios. In addition, average modelled August stream water temperature was obtained for all sites from the NorWeST database, which contains historical and predicted future water temperatures for streams throughout much of the western USA (Isaak et al., 2017). Historical values for August mean stream water temperatures were generated for all sites with data over an 19-year span (1993–2011). Future mean stream temperature values were predictions for 2080 (average of 2070–2099) and were based on projected changes in August air temperature and stream discharge for the A1B greenhouse gas emissions trajectory (Intergovernmental Panel on Climate Change, 2014; Isaak et al., 2017). Water temperatures (historical and future) from NorWeST were not included in species distribution models since future projections were only available for the A1B scenario, which was based on a balanced emphasis on all energy sources, unlike several of the RCP scenarios. In addition, past and future NorWeST water temperature values were based on different dates from the bioclimatic variables; that is, 1993–2011 versus 1960–1990 for historical predictions, and 2070–2099 versus 2061–2080 for future predictions. However, NorWeST water temperature data were used to help determine the extent of projected loss of cold-water habitat throughout the study area (Figure 1).

2.4 | Species distribution models

The relationship between taxon occurrence and climatic predictors and slope were analysed with SDMs using R (R Core Team, 2020). These models were generated with general boosting models (GBMs) and random forest (RF) algorithms using the biomod2 package (Thuiller et al., 2020). For each taxon, SDMs were run using historical data and 2070 RCP scenarios separately for three different climate models. Therefore, results reported here for each taxon and RCP scenario are mean probability of occurrence (POC) values from multiple runs (described below) for two separate algorithms (GBM and RF) from each of the three different climate models used.

The performance of each model run was assessed with a cross-validation approach, where models were fitted four times by using a random sample of 70% of the data and subsequently evaluated against the remaining 30%. For GBM, the default maximum of 2,500 trees, interaction depth of 7.0, and learning rate of 0.001 were used. For RF, the default maximum of 500 trees and node size of 5 was used. Across the four runs, the average area under the curve (AUC) of the receiver operating characteristic was used to estimate strength of model prediction and only RCP projections with an average AUC ≥ 0.7 were evaluated. Estimates of model transferability (Wenger & Olden, 2012) were also obtained by partitioning the historical data non-randomly using fivefold cross-validation and generating AUC values across five separate runs for RF and GBM.

Model output included POC values for historical and 2070 conditions. A 'change in POC' was calculated by subtracting POC in the future from POC in the past. This change in probability was then expressed as a percentage. All sites where a taxon had an average absolute change in POC < 5% were assumed to display no significant change and were classified as displaying no change.

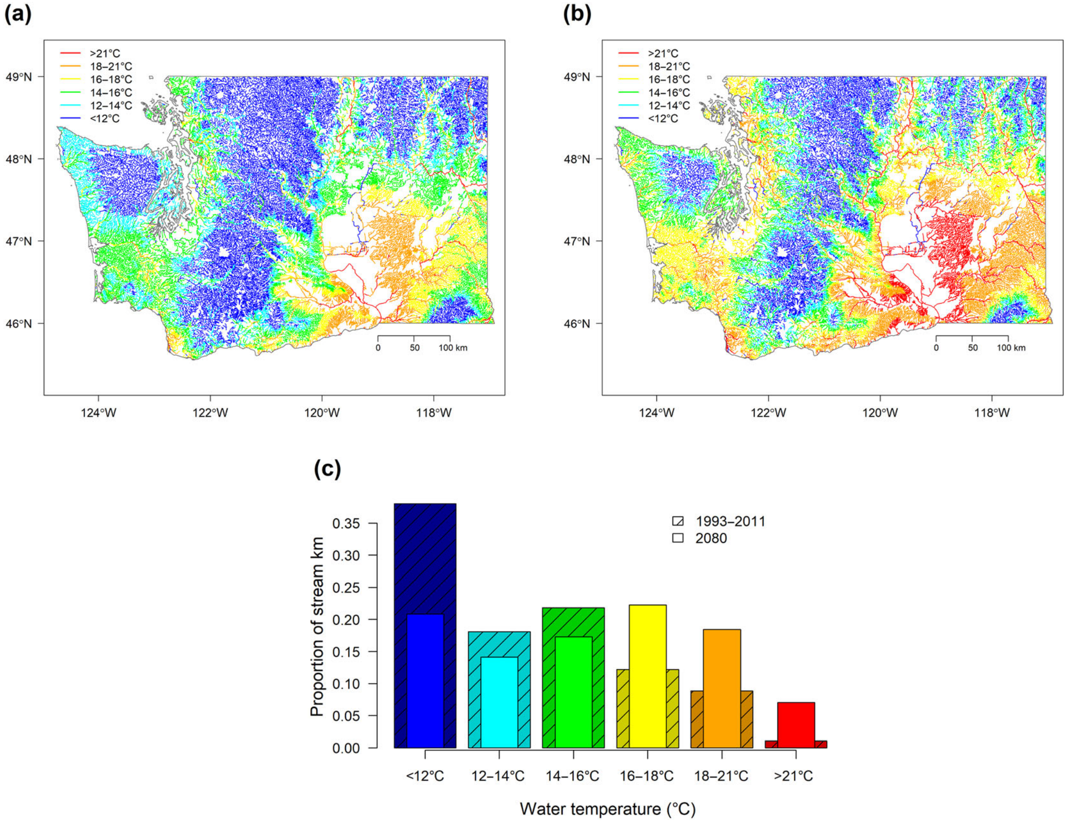

FIGURE 1 NorWeST stream temperature. Mean August stream temperatures for Washington State. (a) Historical temperature 1993–2011, (b) A1B warming trajectory 2080, and (c) proportion of stream kilometres in various temperature ranges in 1993–2011 compared with those predicted for 2080

The relative contribution of each of the variables in model prediction was also tested via randomization with biomod2. The procedure uses correlation between standard predictions and predictions where the variable under investigation has been randomly permutated (Thuiller et al., 2009). If the correlation is high, then there is little difference between the two predictions and the variable is not considered important for the model (Thuiller et al., 2009). This process was repeated five times and the mean correlation coefficient over the runs was calculated.

2.5 | Taxon richness and beta diversity

For each SDM run, POC values were converted to presence/absence using an optimized cut-off value of POC generated in biomod2 (Thuiller et al., 2009). Taxonomic richness (α-diversity) was calculated for each site for the present day and the four RCP scenarios when POC values were greater than cut-off values. Beta diversity was calculated for the present day and each RCP scenario using the presence/absence matrices, and the Sørensen index was calculated for a random subset of one-third of the sites and repeated with 999 permutations.

2.6 | Taxa distribution changes relative to historical trends

To determine whether there were significant differences in spatial distribution between the four RCP scenarios, a blocked analysis of variance was used with percentage change in POC for each of the 23 vertebrate aquatic taxa in the analysis as the dependent variable, whereas the four RCP scenarios were the independent factor and species was the blocked effect. Tukey's pairwise comparisons tested for differences between RCP scenarios. The 95% confidence intervals (CIs) of differences in mean values were used to test for differences between RCP scenarios for taxon richness and beta diversity.

3 | RESULTS

3.1 | NorWeST stream water temperatures and climatic variables

According to the NorWeST stream temperature model, water temperatures are predicted to increase considerably with climate change in various parts of the study region, leading to a substantial loss of cold-water refugia (Figure 1a,b). The proportion of stream kilometres in Washington State with mean August water temperatures below 12°C will decline by 45.2% (from 0.380 to 0.209) by 2080, and those in the range 12–14°C and 14–16°C will decline by 22.0% (from 0.181 to 0.141) and 20.7% (from 0.218 to 0.173) respectively (Figure 1c). Concurrently, the proportion of stream kilometres with mean August water temperatures above 16°C will increase considerably, with temperatures in the range 16–18°C, 18–21°C, and >21°C projected to increase by 83% (from 0.122 to 0.223), 108.4% (from 0.088 to 0.184), and 581.6% (from 0.010 to 0.070) respectively.

Among the five climate variables used in the SDMs, mean values generally differed from historical values for most climate models and all RCP scenarios (Table 1). With very few exceptions, temperatures increased and precipitation decreased with RCP scenarios. In addition, the seasonality of temperature and precipitation increased with RCP scenarios. Values for slope (unitless from NHDplus) ranged from 0 to 0.3892.

3.2 | Taxon distribution changes relative to historical trends

All SDM models had mean ROC values >0.7 (mean values ranged from 0.71–0.97) across climate models based on in-sample validation, indicating good fit (Swets, 1988). Transferability was good (>0.70) or excellent (>0.90) for 18 of the 23 taxa evaluated, with three of the four remaining taxa having mean AUC values >0.60 (Table 2). Only *Cottus confusus* had mean transferability AUC values <0.60. Across the four 2070 RCP scenarios, 61–70% taxa were predicted to experience an increase, 17–22% a decrease, and 13–22% no change in POC (Figure 2). Regarding differences in overall changes in POC values between RCP scenarios, pairwise comparisons were significantly different from one another ($P < 0.05$) for all RCP scenarios except between RCP 6.0 and 8.5 (Table 3). Notably, the average increase in POC for RCP 6.0 and RCP 8.5 over that of RCP 2.6 was 6.38% and 8.20% respectively. The net change in POC values (Figure 3) showed that, across the four RCP scenarios, the four taxa *Oncorhynchus clarkii*, *Ascaphus*, *Cottus rhotheus*, and *Oncorhynchus mykiss* consistently showed a net decrease in POC, whereas the remaining taxa were predicted to experience a net increase or little net change in POC.

When plotting the predicted response at individual sites for each of the vertebrate taxa evaluated, interesting patterns emerged in 2070 under the RCP 8.5 scenario (Figure 4 (selected taxa); Supporting Information Figures S8–S15 (all taxa)). For example, some taxa, such as *Ptychocheilus oregonensis*, were expected to increase in POC across much of the study area (Figure 4a,b). Other taxa, such as *Dicamptodon*, were expected to experience either a range shift (Figure 4c,d) or to decrease, such as *O. clarkii*, across much of the study area (Figure 4e,f). More specifically, suckers, minnows, most sculpins, and mountain whitefish were predicted to experience large increases in their distribution based on POC (Supporting Information Figures S8–S15). Other taxa, such as *Ascaphus* (tailed-frog) and *O. clarkii* (cutthroat trout), were anticipated to experience considerable decreases in POC across Washington State (Supporting Information Figures S8–S15). Some taxa, such as *Dicamptodon* spp. (Pacific giant salamanders), Petromyzontidae (members of the lamprey family), and *Salvelinus*

TABLE 1 Mean and range of values observed for the five bioclimatic variables and slope used in the species distribution models for each climate model and representative concentration pathway (RCP) scenario

Climate model	RCP	Annual mean temperature (BIO1)	Temperature seasonality (BIO4)	Maximum air temperature of warmest month (BIO5)	Precipitation of the driest month (BIO14)	Precipitation seasonality (BIO15)	Slope
Historical (1960–1990)		79.3	5,977.2	242.0	29.7	52.7	0.0357
		6.2–117.8	3,551–8,964	175.6–321.8	5.0–67.6	21.3–75.50	0–0.3892
NorESM1-M (2070)	2.6	96.7	6,331.2	266.6	29.6	59.1	
		26.8–137.8	3,802.3–9,291.5	200.2–350.8	5.0–64.4	23.2–80.5	
	4.5	103.2	6,313.3	282.0	27.2	56.1	
		34.0–147.0	3,677.8–9,309.0	217.6–364.8	3.5–62.6	22.3–76.5	
	6.0	103.6	6,390.3	275.3	23.6	64.1	
		34.8–145.2	3,744.8–9,427.2	208.6–361.4	4.0–53.6	28.8–86.5	
	8.5	114.7	6,748.6	299.4	18.4	62.4	
		48.6–159.0	3,949.3–9,816.5	231.4–387.8	3.0–42.8	33.2–81.5	
CCSM4 (2070)	2.6	96.2	6,016.1	262.2	26.5	55.3	
		25.6–134.0	3,516.7–8,952.8	196.2–346.8	5.0–54.8	25.2–77.0	
	4.5	103.9	6,130.0	277.2	22.8	58.5	
		35.4–142.7	3,435.0–9,008.2	211.2–364.8	4.0–51.6	26.3–79.5	
	6.0	103.8	6,353.1	281.0	22.3	56.3	
		35.8–143.0	3,501.8–9,222.0	212.1–368.8	3.8–53.6	26.0–77.2	
	8.5	116.2	6,373.3	297.3	22.4	60.6	
		49.8–156.3	3,399.3–9,251.2	222.8–389.8	3.8–50.6	28.2–82.0	
MPI-ESM-LR (2070)	2.6	95.4	5,809.9	256.0	37.3	50.0	
		24.6–133.0	3,410.3–8,656.5	191.2–332.8	7.0–76.0	21.0–71.8	
	4.5	103.0	5,942.7	268.6	30.5	51.0	
		32.8–142.0	3,468.6–8,713.8	204.2–349.8	6.0–67.4	20.8–73.2	
	8.5	115.8	6,163.5	290.6	27.6	54.1	
		47.6–156.0	3,612.1–8,841.8	225.8–369.2	5.0–53.0	26.8–74.8	

fontinalis (brook trout) were predicted to see shifts in their distributions rather than a general increase or decrease. Both lampreys and Pacific giant salamanders were projected to have lower POC along the Cascade Range, but higher POC in the Coast Range (Supporting Information Figures S8–S15).

3.3 | Taxon richness and beta diversity

Relative to historical conditions, taxon richness was expected to increase across RCP scenarios by an average of 2.88 (95% CI, 2.78–2.99), 3.13 (3.04–3.22), 4.19 (4.05–4.32), and 5.14 (5.02–5.25) taxa for RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5 respectively (Figure 5a). Beta diversity decreased relative to historical conditions across RCP scenarios (Figure 5b). All scenarios differed from one another, with the lowest beta diversity observed at RCP 8.5 (95% CI, RCP 2.6 (0.584–0.593), RCP 4.5 (0.531–0.543), RCP 6.0 (0.481–0.491), RCP 8.5 (0.392–0.408)).

3.4 | Relative importance of climatic variables and slope

Temperature had the highest relative importance across all taxa, followed by slope and precipitation (Figure 6a), yet the relative importance of the different variables in predicting future spatial distributions varied widely among species (Figure 6b). A combination of variables explained future distributions for all taxa, yet for some taxa, such as *Catostomus macrocheilus*, *Prosopium williamsoni*, *Rhinichthys cataractae* (longnose dace), *P. oregonensis* (northern pikeminnow) *Oncorhynchus tshawytscha* (chinook salmon), and *Cottus asper* (prickly sculpin), slope had the highest relative importance. In addition, temperature variables had the highest relative importance for most taxa, such as *Catostomus columbianus*, *S. fontinalis* (brook trout), *Oncorhynchus kisutch* (coho salmon), *O. clarkii*, *Gasterosteus aculeatus* (three-spined stickleback), *Cottus perplexus/gulosus*, and *Ascaphus* spp. Conversely, precipitation was predicted to have the highest relative importance for other taxa, such as *Cottus bairdii*, *Cottus beldingii* (paiute sculpin), and *C. confusus* (shorthead sculpin).

TABLE 2 Area under the curve of the receiver–operator characteristic plot for models based on in-sample validation (range of values across climate models) and transferability assessment (non-random fivefold cross-validation). Species distribution models run using random forest (RF) and general boosting model (GBM)

Taxon	In-sample GBM	In-sample RF	Transferability-fivefold GBM	Transferability-fivefold RF
Ascaphus	0.941–0.944	0.944–0.946	0.876	0.879
Catostomus columbianus	0.884–0.962	0.866–0.948	0.906	0.878
Catostomus macrocheilus	0.84–0.888	0.833–0.886	0.869	0.835
Cottus aleuticus	0.876–0.9	0.884–0.914	0.816	0.814
Cottus asper	0.77–0.836	0.759–0.83	0.739	0.665
Cottus bairdii	0.794–0.846	0.78–0.876	0.768	0.738
Cottus beldingii	0.918–0.928	0.908–0.938	0.759	0.777
Cottus confusus	0.672–0.731	0.677–0.74	0.562	0.547
Cottus perplexus/gulosus	0.958–0.975	0.963–0.974	0.901	0.934
Cottus rhotheus	0.83–0.85	0.832–0.858	0.716	0.723
Dicamptodon	0.882–0.912	0.865–0.907	0.698	0.725
Gasterosteus aculeatus	0.854–0.87	0.867–0.887	0.762	0.764
Oncorhynchus clarkii	0.81–0.858	0.813–0.85	0.725	0.726
Oncorhynchus kisutch	0.877–0.892	0.878–0.891	0.848	0.865
Oncorhynchus mykiss	0.769–0.769	0.76–0.76	0.631	0.643
Oncorhynchus tshawytscha	0.756–0.771	0.719–0.746	0.657	0.607
Petromyzontidae	0.856–0.861	0.854–0.864	0.809	0.815
Prosopium williamsoni	0.794–0.896	0.824–0.879	0.805	0.758
Ptychocheilus oregonensis	0.898–0.944	0.907–0.939	0.884	0.862
Rhinichthys cataractae	0.733–0.787	0.754–0.797	0.659	0.604
Rhinichthys osculus	0.882–0.895	0.866–0.89	0.776	0.762
Richardsonius balteatus	0.889–0.894	0.892–0.91	0.830	0.796
Salvelinus fontinalis	0.852–0.903	0.873–0.922	0.781	0.768

4 | DISCUSSION

4.1 | RCP scenarios influence stream vertebrate distributions

Results from the analyses on an extensive dataset collected in Washington State over 24 years shows that the spatial distributions of many stream vertebrate taxa will shift by 2070 in response to climate change, when the greatest overall changes are projected to occur under the RCP 6.0 and RCP 8.5 scenarios. Across the 23 taxa evaluated, the change in POC for RCP 6.0 and RCP 8.5 averaged 6.4–8.2% and 3.4–5.3% greater than would be expected under RCP 2.6 and RCP 4.5 respectively. The implications are that, unless policy decisions are made that are focused on greatly reducing greenhouse gas emissions, the climate change impacts forecasted by our models will result in altered composition of stream vertebrate communities in 2070. Under each of the RCP scenarios, none of the taxa evaluated are likely to disappear completely from their historical ranges by 2070, although *O. clarkii* is projected to decrease considerably across much of its historical range in Washington State. Instead, most taxa can be expected to experience considerable alterations in spatial distribution relative to historical conditions in agreement with earlier reports (Buisson et al., 2008; Comte et al., 2013; Pound, Larson & Passy, 2021). Also consistent with Pound, Larson & Passy (2021), greater taxon richness is projected across RCP scenarios as the majority of taxa are predicted to increase in prevalence in 2070. These findings highlight that regional studies such as this one provide an important complement to continental surveys of species distributions. They also show that, to gain greater insights into the complex relationships that stream fauna have with predicted climate changes, multiscale investigations are necessary. Regional studies have much finer resolution and are better suited for assessing small-scale variability, which also allows more detailed evaluations of individual taxon responses, which can inform the development of conservation plans.

4.2 | Variation in taxon responses to climate change

One of the substantial findings for fish species reported in Pound, Larson & Passy (2021) was a predicted increase in species of minnows (Cyprinidae) and a dramatic decrease in several salmonid species

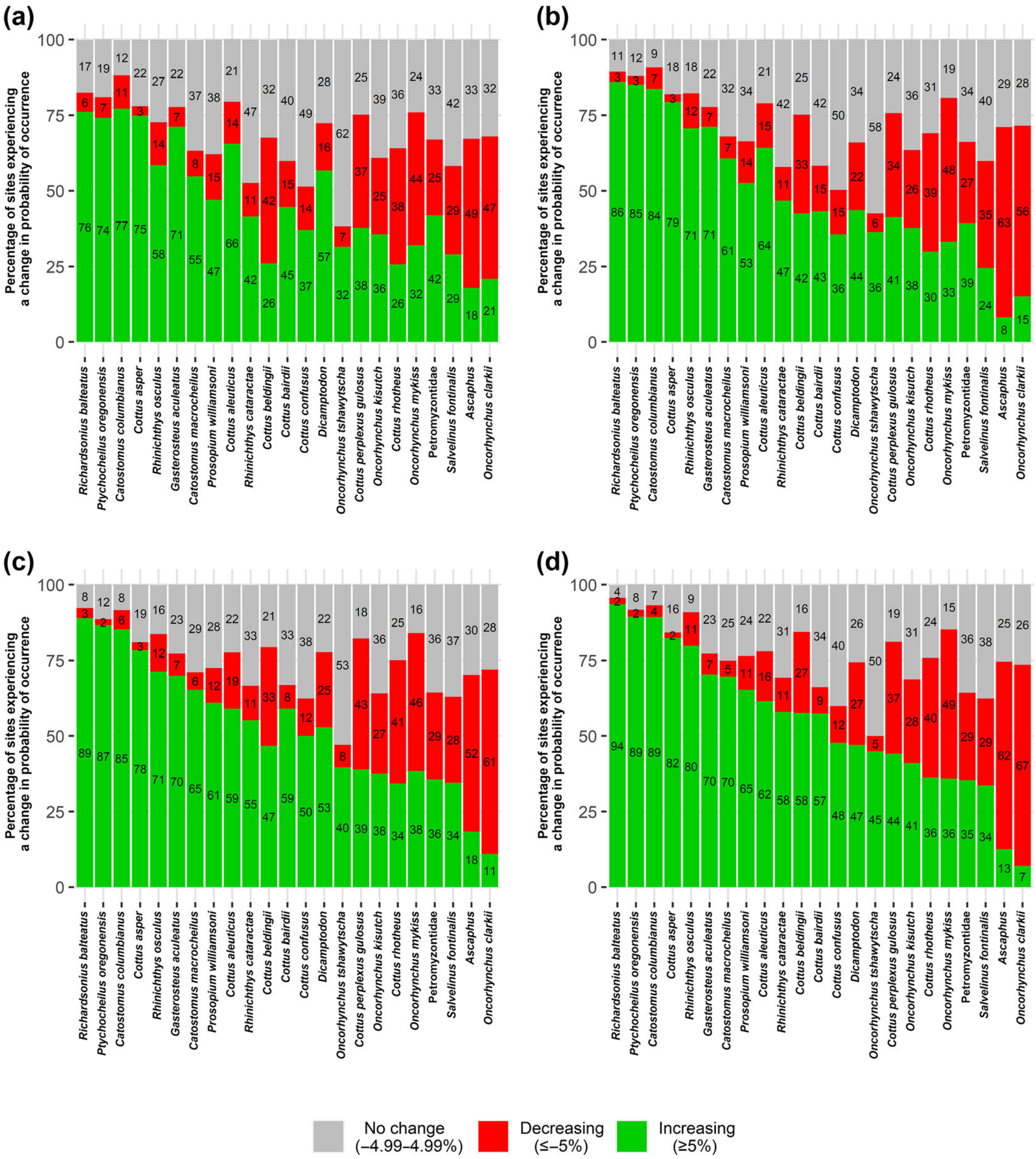

FIGURE 2 Predicted spatial distributions of stream vertebrates in 2070 for (a) RCP 2.6, (b) RCP 4.5, (c) RCP 6.0, and (d) RCP 8.5. Taxa are organized in descending order based on their positive change in probability of occurrence under RCP 8.5. RCP: representative concentration pathway

TABLE 3 Tukey pairwise comparisons between various representative concentration pathway (RCP) scenarios for percentage change in 2070 compared with historical conditions (i.e. increase + decrease)

Scenario comparison	Difference	Lower	Upper	Adjusted *P*-value
RCP 4.5–RCP 2.6	2.95	0.67	5.23	0.0060
RCP 6.0–RCP 2.6	6.38	4.10	8.66	0.0000
RCP 8.5–RCP 2.6	8.20	5.92	10.48	0.0000
RCP 6.0–RCP 4.5	3.43	1.15	5.71	0.0010
RCP 8.5–RCP 4.5	5.25	2.97	7.53	0.0000
RCP 8.5–RCP 6.0	1.82	−0.46	4.10	0.1621

Note: Blocked analysis of variance revealed significant main effects of RCP scenarios ($F_{3,66} = 68.28$, $P < 0.000001$). The four RCP scenarios were used as the independent factor and species as the blocked factor. Lower and upper are values of 95% confidence interval of difference between means.

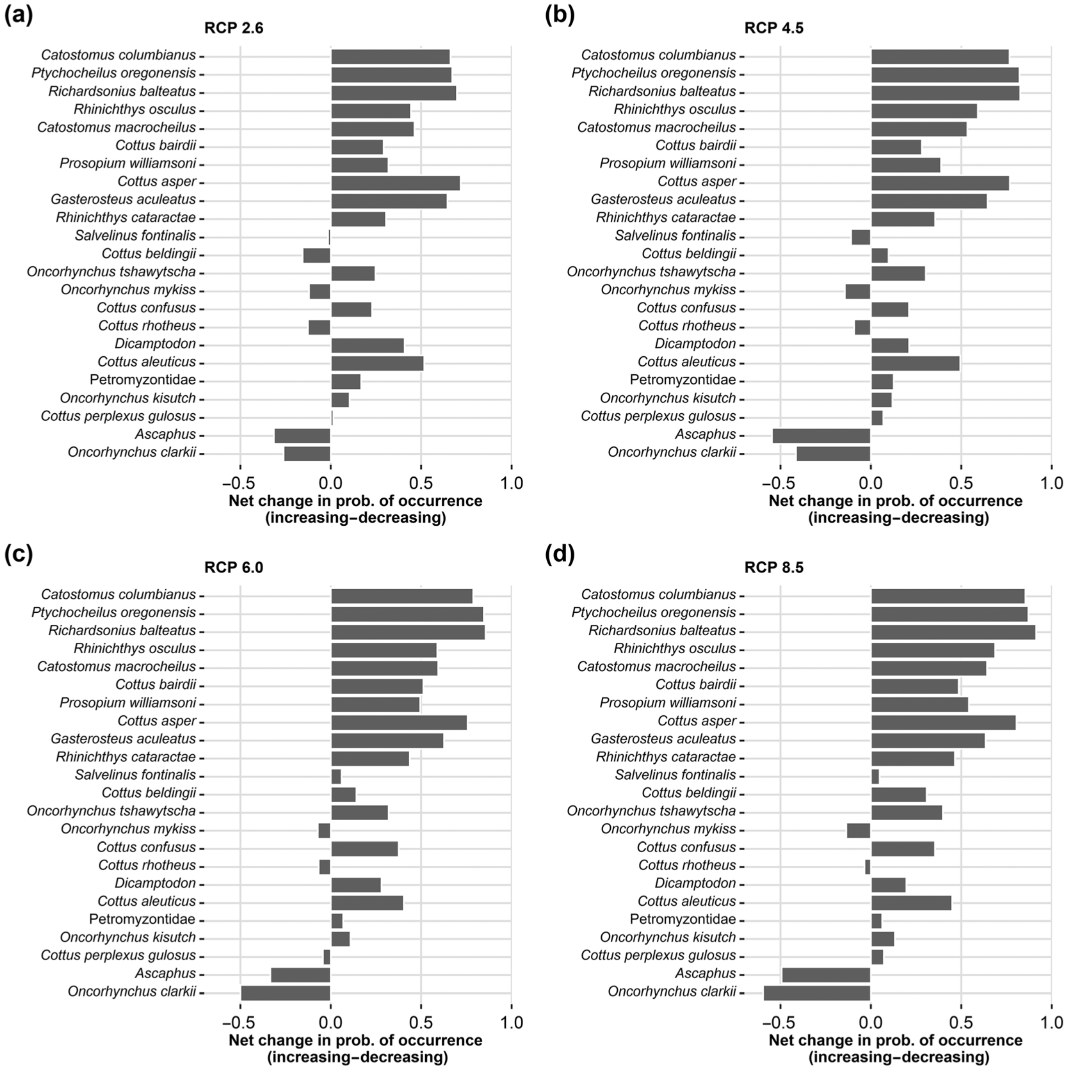

FIGURE 3 Net change in probability of occurrence in taxon distributions in 2070 relative to historical trends for (a) RCP 2.6, (b) RCP 4.5, (c) RCP 6.0, and (d) RCP 8.5. RCP: representative concentration pathway

across the conterminous USA. Similar trends for minnows were observed in this study, but at a smaller spatial scale, with a predicted increase in distribution for several species of minnows as well as suckers and most sculpins. Unlike Pound, Larson & Passy (2021), the findings for salmonids in this study were mixed, with several taxa predicted to decrease and others to increase by 2070. Other studies have also projected a decline of salmonids resulting from climate change (Wenger et al., 2011; Ruesch et al., 2012), but results from this study suggest that the response of salmonids may be more subtle, as well as taxon or region specific. Two of the salmonid taxa forecasted to decrease in this study area were *O. clarkii* and *O. mykiss*. *Oncorhynchus clarkii* has a relatively low upper temperature tolerance and low optimum growth temperature, which make it very susceptible to temperature increases (Bear, McMahon & Zale, 2007), and *O. mykiss* was also predicted to decrease by Pound, Larson & Passy (2021) and by Wenger et al. (2011). Other salmonids evaluated in this analysis — *S. fontinalis*, *O. kisutch*, *O. tshawytscha*, and *P. williamsoni* — were all predicted to increase in POC by 2070, although only very modest net increases across RCP scenarios were predicted for *S. fontinalis* and *O. kisutch*. This is in contrast with studies finding *S. fontinalis* to decline considerably across the USA (Pound, Larson & Passy, 2021) or in parts of the intermountain western USA. (Wenger et al., 2011). Results for *P. williamsoni* were also contrary to previous work reporting population-level declines in some rivers in the USA (Boyer et al., 2017), which could be linked to their low upper thermal tolerance (Brinkman, Crockett & Rogers, 2013).

A potential explanation for the discrepancy in predicted responses among certain salmonids could be that enough pockets of cool water will still remain to allow the persistence of these taxa (Isaak et al., 2016). Although climate change will certainly result in considerable loss of very cold water stream habitat within the present study area, there may still be enough cool-water habitat remaining in 2070 to help buffer some of the effects of warming from climate

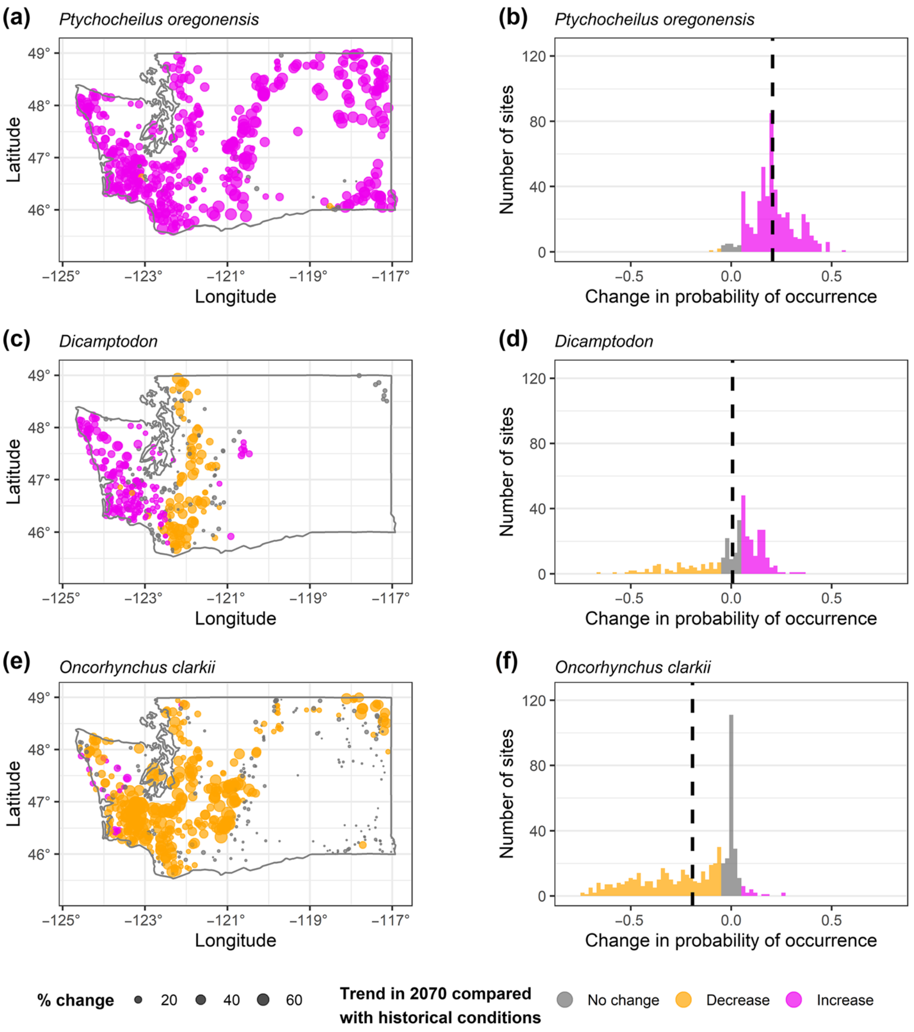

FIGURE 4 Forecasted trends in spatial distributions in 2070 under representative concentration pathway 8.5 relative to historical conditions for representative vertebrate taxa that are (a, b) predicted to increase considerably in probability of occurrence, (c, d) experience a range shift, or (e, f) decrease considerably in probability of occurrence. Figures for all vertebrate taxa in this study can be found in Supporting Information Figures S8–S15

change for some salmonids. It is also possible that these more subtle differences for certain taxa were only detected because of a higher density of sites in this study region, covering a broader variety of environmental conditions than found in the continental study (Pound, Larson & Passy, 2021). The impacts of climate change on salmonids have been shown to be quite variable, with positive and negative effects possible (Leppi et al., 2014); yet even though some salmonid taxa were predicted to experience a net increase in this study, there were regions where several taxa were also predicted to decline. For example, *S. fontinalis* was forecasted to decrease in north-east Washington, where it is currently most abundant, but to increase in other parts of the state where this species is at present rare or absent. Also, *O. kisutch* was forecasted to decrease in much of western Washington where stream temperatures could approach major physiological thresholds of 21°C. The results for *O. tshawytscha* should be interpreted cautiously as the data come largely from wadeable streams and counts were of juvenile fish rather than adults, whereas this species typically spawns in larger systems and spends a relatively large portion of its life in the ocean and estuaries, which were not modelled here.

Although the SDM approach used examined individual taxon responses, the implications are that the predicted changes observed are likely to result in altered biotic interactions and food-web structure through expansion of non-native species, competition, and predation (Zanden, Casselman & Rasmussen, 1999; Van Zuiden et al., 2016). Range expansion by *S. fontinalis*, which was introduced to western North America and has a fast initial growth rate and high fecundity (Karas, 2015), could have further adverse impacts on native salmonid taxa and has been documented to hybridize with threatened *Salvelinus confluentus* (Leary, Allendorf & Forbes, 1993; Kanda, Leary & Allendorf, 2002; Taniguchi et al., 2011). In addition, *O. mykiss* has been reported to have a higher upper temperature tolerance and greater growth capacity than, for example, *O. clarkii*, which could account for reports that it has successfully displaced westslope cutthroat at lower elevation sites in the western USA (Bear, McMahon & Zale, 2007). Furthermore, *P. oregonensis*, a native to north-western North America, but also a voracious predator of migrating salmonids (Beamesderfer, Ward & Nigro, 1996), has the potential to increase its rates of predation with increasing stream temperatures (Petersen & Kitchell, 2001). Therefore, it is likely that

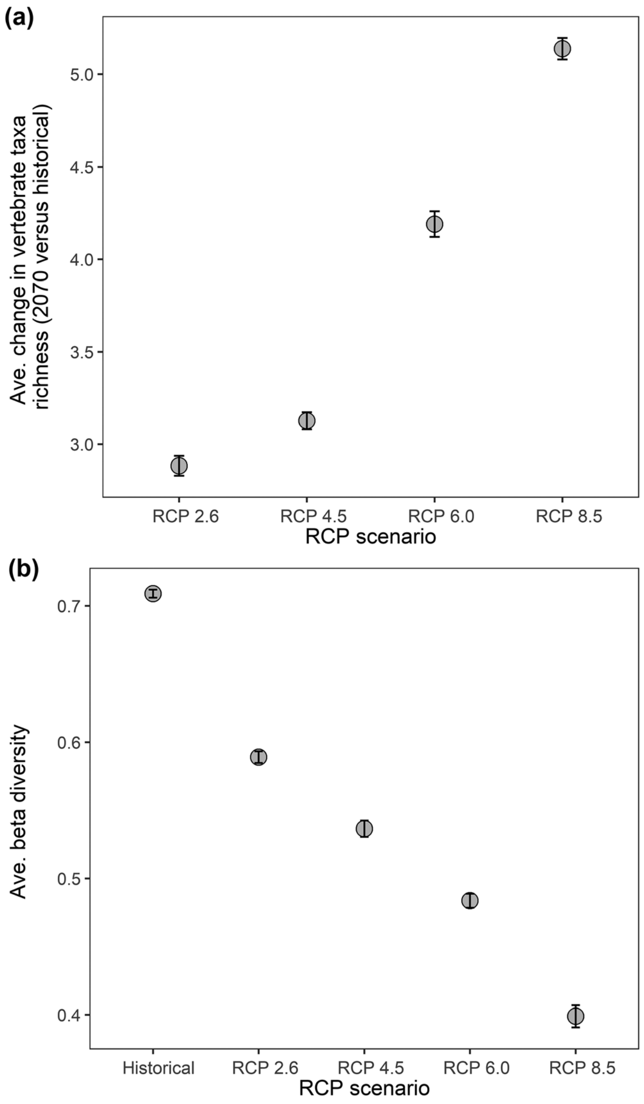

FIGURE 5 (a) Average change in taxa richness from historical values and (b) beta diversity for historical and each of the representative concentration pathways (RCPs) for stream vertebrates in 2070. Error bars are ±1 *SE*

climate change will influence interspecific interactions that could lead to significantly altered stream communities and biological integrity.

The results for biodiversity support these conclusions as they transcend specificity of regional faunas and are thus broadly comparable. Predicted trends in taxon richness showed an increase under all RCP scenarios, particularly under RCP 8.5, with an average increase of more than five additional taxa over historical conditions. This suggests that more severe changes in temperature and precipitation may lead to greater changes in taxon richness. Milder winter conditions and warmer water temperatures, especially in colder than optimal, high-elevation systems (Leppi et al., 2014), have the capacity to increase the availability of habitats that were previously uninhabitable for certain taxa. Furthermore, beta diversity decreased considerably among all RCP scenarios, with the greatest change under RCP 8.5. These results suggest that higher taxon richness is associated with reduced compositional dissimilarity among stream vertebrate communities (i.e. biotic homogenization), consistent with Su et al. (2021) and Pound, Larson & Passy (2021).

Notable trends were also observed for the two species of amphibians included in this study. *Dicamptodon* spp. were predicted to experience a shift in future distributions, with a lower POC along the Cascade Range and a higher POC along the Coast Range. The other amphibian evaluated, *Ascaphus* (tailed-frog), is a habitat specialist, requiring cold and clear fast-flowing water for mating, egg-laying, and larval development; its long aquatic residency makes it vulnerable to channel disturbances. Therefore, loss of spawning habitat due to human disturbances and climate change could lead to its decline or eventual extinction. Findings from the two amphibian taxa examined are consistent with other observations that amphibians may be good indicator/sentinel species for evaluating the impacts of climate change on stream communities (Winter et al., 2016).

4.3 | Relative influence of local and climatic variables varies by taxon

In addressing the third objective of this study, no single variable came out as being more important across all the taxa studied. Instead, responses were species dependent and influenced by a combination of factors, yet temperature was the most prevalent across taxa. However, even among the temperature variables examined, no consistent pattern emerged with maximum temperature of the warmest month important for *C. columbianus*, and temperature seasonality important for *S. fontinalis*, *Dicamptodon*, and *O. kisutch*. A similar pattern was observed for precipitation, with precipitation of the driest month the most important variable for *C. beldingii*, but precipitation seasonality for *C. confusus*. Even for taxa where slope had the highest relative importance, climate impacts will still influence future distributions of these taxa. Climate-induced changes in precipitation patterns and flow regimes (Intergovernmental Panel on Climate Change, 2014) will further affect sensitive cold-water taxa (Mantua, Tohver & Hamlet, 2010). For example, *Ascaphus* and juvenile *O. kisutch* not only require cold water but are also sensitive to changes in flow regimes and sedimentation (Dupuis & Friele, 2006). The family Petromyzontidae is another taxon that is sensitive to climate-induced changes in water temperature and hydrology, which can affect multiple life stages of these organisms (Wang et al., 2020). Thus, the future distributions of stream vertebrate taxa will be the consequence of a complex combination of factors.

4.4 | SDM considerations

The SDM results presented here can provide important insights into how climate change may influence vertebrate stream taxa in temperate and semi-arid climates, but they also need to be interpreted with certain caveats. For example, some potential habitats may not be accessible to species because of natural or anthropogenic barriers,

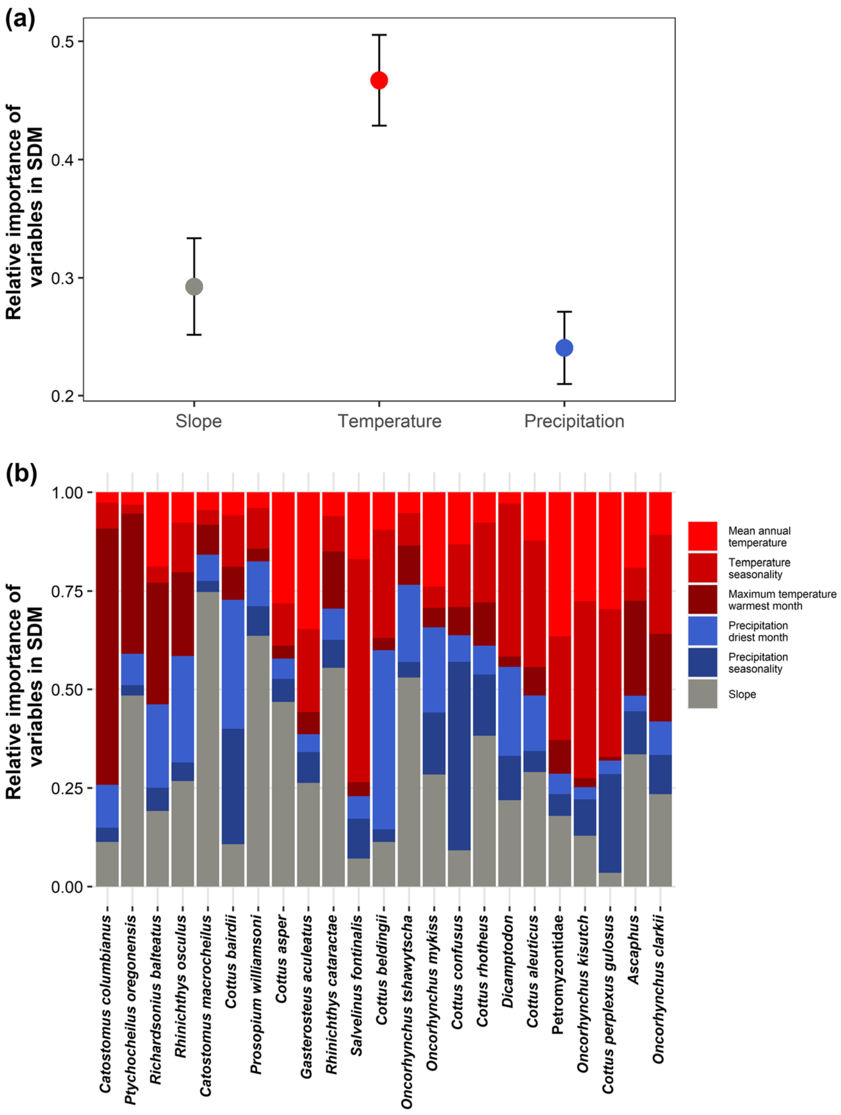

FIGURE 6 Relative importance of variables in the species distribution models (SDMs) for each taxon. Temperature variables include annual mean air temperature, air temperature seasonality, and maximum air temperature of the warmest month from WoldClim. Precipitation variables include precipitation of the driest month and precipitation seasonality from WorldClim. Local variable included slope. (a) Relative importance of predictor variables grouped as local or climatic variables. (b) Relative importance of predictor variables by taxa

which were not evaluated here. In addition, the SDMs developed here were correlative species distribution models that can sometimes yield different predictions from process-based models (Higgins et al., 2020). Despite these caveats, the results showed good to excellent model fits for all taxa and good to excellent transferability for most taxa, suggesting that results from SDM models can be useful for informing the development of management plans for vulnerable taxa.

4.5 | Implications for conservation

Stream habitats with very cold water (<12°C) are expected to decline considerably by 2070. This large decrease in cold-water refugia will have adverse consequences for obligate cold-water taxa; yet, as results presented here show, there may still be enough cold-water refugia remaining to buffer some of the effects of warming, consistent with Isaak et al. (2016). Identifying and protecting habitat and hydrology that can provide thermal refugia to sensitive cold- and cool-water aquatic vertebrate taxa may be critical for their long-term persistence (Williams et al., 2011; Armstrong & Schindler, 2013; Ebersole et al., 2020). Exceptionally cold stream inputs in the headwaters have been observed to sustain populations of native salmonids, and species population decline has also been observed to proceed more slowly in these very cold habitats despite climate warming (Isaak et al., 2015; Isaak et al., 2016). This is probably because, so far, these streams have been less sensitive to direct temperature increases, and thus naturally buffered from climate change (Luce et al., 2014; Isaak et al., 2016). Moreover, it is also harder for invasive species to invade these extremely cold environments (Isaak et al., 2016), which may serve as sources for populations to resupply habitats downstream (Heino et al., 2015). Therefore, protecting and maintaining aquatic vertebrate populations in these cold invasion-resistant habitats should require less costly management interventions and could also provide a foundation for conservation planning to maintain broader species distributions for the future (Isaak et al., 2015). Better knowledge of which areas may become suitable under climate change can be invaluable for conservation (Olden et al., 2011). This knowledge may prove to be especially useful for conservation efforts exploring the use of assisted migration for fish rescue (Olden et al., 2011).

For streams not buffered by very cold water inputs or those in more heavily affected areas, developing or enhancing existing riparian cover could help to minimize the impacts of rising temperatures. In addition, enhancing groundwater–surface water connectivity could be accomplished through measures that contribute to greater sinuosity, pool development, and inputs of large wood, which may help to buffer elevated water temperatures and increase water storage. Reintroducing beaver where possible or mimicking their impacts on streams could also help with water storage moderation of stream water temperatures (Weber et al., 2017). The results reported here indicate greater impacts with higher carbon emissions, suggesting that efforts aimed at curbing emissions could greatly help protect and conserve stream vertebrate communities as well as other biotic communities in temperate and semi-arid ecosystems.

Mitigation to protect freshwater vertebrates will require decisions to be made at local, state, federal and international levels. Evaluating the results from SDM studies conducted at a variety of spatial scales can help resource managers and planners to better understand the potential impacts of climate change on stream vertebrates so that plans can be developed for protecting sensitive taxa, managing economically and culturally important taxa, and maintaining biological integrity. Stream ecosystems are influenced by a variety of stressors in addition to climate change, including human development, pollution, and species introductions. This means that multiple interest groups will have to work together, using novel modelling and management approaches to preserve the biological integrity of stream assemblages.

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CONFLICT OF INTEREST

All authors declare no conflicts of interest/competing interests.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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REFERENCES

Allen, G.H. & Pavelsky, T.M. (2018). Global extent of rivers and streams. *Science*, 361(6402), 585–588. https://doi.org/10.1126/science.aat0636

Alofs, K.M., Jackson, D.A. & Lester, N.P. (2014). Ontario freshwater fishes demonstrate differing range-boundary shifts in a warming climate. *Diversity and Distributions*, 20(2), 123–136. https://doi.org/10.1111/ddi.12130

Antão, L.H., Bates, A.E., Blowes, S.A., Waldock, C., Supp, S.R., Magurran, A.E. et al. (2020). Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nature Ecology and Evolution*, 4(7), 927–933. https://doi.org/10.1101/841833

Armstrong, J.B. & Schindler, D.E. (2013). Going with the flow: Spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. *Ecosystems*, 16(8), 1429–1441. https://doi.org/10.1007/s10021-013-9693-9

Babaluk, J.A., Reist, J.D., Johnson, J.D. & Johnson, L. (2000). First records of sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) from Banks Island and other records of Pacific salmon in Northwest Territories, Canada. *Annales Zoologici Fennici*, 53(2), 161–164. https://doi.org/10.2307/40512204

Baiser, B., Olden, J.D., Record, S., Lockwood, J.L. & McKinney, M.L. (2012). Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society B: Biological Sciences*, 279(1748), 4772–4777. https://doi.org/10.1098/rspb.2012.1651

Beamesderfer, R.C., Ward, D.L. & Nigro, A.A. (1996). Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(12), 2898–2908. https://doi.org/10.1139/f96-225

Bear, E.A., McMahon, T.E. & Zale, A.V. (2007). Comparative thermal requirements of westslope cutthroat trout and rainbow trout: Implications for species interactions and development of thermal protection standards. *Transactions of the American Fisheries Society*, 136(4), 1113–1121. https://doi.org/10.1577/t06-072.1

Boyer, J.K., Guy, C.S., Webb, M.A.H., Horton, T.B. & McMahon, T.E. (2017). Reproductive ecology, spawning behavior, and juvenile distribution of mountain whitefish in the Madison River, Montana. *Transactions of the American Fisheries Society*, 146(5), 939–954. https://doi.org/10.1080/00028487.2017.1313778

Brinkman, S.F., Crockett, H.J. & Rogers, K.B. (2013). Upper thermal tolerance of mountain whitefish eggs and fry. *Transactions of the American Fisheries Society*, 142(3), 824–831. https://doi.org/10.1080/00028487.2013.765503

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & Ecology, G.W. (2004). Towards a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789. https://doi.org/10.1890/03-9000

Buisson, L., Grenouillet, B., Casajus, N. & Lek, S. (2010). Predicting the potential impacts of climate change on stream fish assemblages. In: *American Fisheries Society Symposium*, Vol. 73, pp. 327–346.

Buisson, L., Thuiller, W., Lek, S., Lim, P. & Grenouillet, G. (2008). Climate change hastens the turnover of stream fish assemblages. *Global Change Biology*, 14(10), 2232–2248. https://doi.org/10.1111/j.1365-2486.2008.01657.x

Comte, L., Buisson, L., Daufresne, M. & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshwater Biology*, 58(4), 625–639. https://doi.org/10.1111/fwb.12081

Comte, L. & Grenouillet, G. (2013). Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography*, 36(11), 1236–1246. https://doi.org/10.1111/j.1600-0587.2013.00282.x

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. et al. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, 105(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105

Dupuis, L. & Friele, P. (2006). The distribution of the Rocky Mountain tailed frog (*Ascaphus montanus*) in relation to the fluvial system: Implications for management and conservation. *Ecological Research*, 21(4), 489–502. https://doi.org/10.1007/s11284-006-0147-0

Ebersole, J.L., Quiñones, R.M., Clements, S. & Letcher, B.H. (2020). Managing climate refugia for freshwater fishes under an expanding human footprint. *Frontiers in Ecology and the Environment*, 18(5), 271–280. https://doi.org/10.1002/fee.2206

Eby, L.A., Helmy, O., Holsinger, L.M. & Young, M.K. (2014). Evidence of climate-induced range contractions in bull trout *Salvelinus confluentus* in a Rocky Mountain watershed, U.S.A. *PLoS ONE*, 9(6), e98812. https://doi.org/10.1371/journal.pone.0098812

Elsner, M.M., Cuo, L., Voisin, N., Deems, J.S., Hamlet, A.F., Vano, J.A. et al. (2010). Implications of 21st century climate change for the hydrology of Washington State. *Climatic Change*, 102(1), 225–260. https://doi.org/10.1007/s10584-010-9855-0

Epstein, J.M., Pine, W.E., Romagosa, C.M., Scott, M.C., Phillips, C.T., Marion, C.A. et al. (2018). State- and regional-scale patterns and drivers of freshwater fish functional diversity in the southeastern USA. *Transactions of the American Fisheries Society*, 147(6), 1179–1198. https://doi.org/10.1002/tafs.10110

Griffiths, D., McGonigle, C. & Quinn, R. (2014). Climate and species richness patterns of freshwater fish in North America and Europe. *Journal of Biogeography*, 41(3), 452–463. https://doi.org/10.1111/jbi.12216

Guisan, A. & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S. & Bini, L.M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. *Freshwater Biology*, 60(5), 845–869. https://doi.org/10.1111/fwb.12533

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, 12(3), 450–455. https://doi.org/10.1111/j.1365-2486.2006.01116.x

Higgins, S.I., Larcombe, M.J., Beeton, N.J., Conradi, T. & Nottebrock, H. (2020). Predictive ability of a process-based versus a correlative species distribution model. *Ecology and Evolution*, 10(20), 11043–11054. https://doi.org/10.1002/ece3.6712

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978. https://doi.org/10.1002/joc.1276

Intergovernmental Panel on Climate Change. (2014). *Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel ON Climate Change*. Geneva, Switzerland: IPCC.

Isaak, D.J., Wenger, S.J., Peterson, E.E., Hoef, J.M.V., Nagel, D.E., Luce, C.H. et al. (2017). The NorWeST summer stream temperature model and scenarios for the western US: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. *Water Resources Research*, 53(11), 9181–9205. https://doi.org/10.1002/2017wr020969

Isaak, D.J., Young, M.K., Luce, C.H., Hostetler, S.W., Wenger, S.J., Peterson, E.E. et al. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences*, 113(16), 4374–4379. https://doi.org/10.1073/pnas.1522429113

Isaak, D.J., Young, M.K., Nagel, D.E., Horan, D.L. & Groce, M.C. (2015). The cold-water climate shield: Delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology*, 21(7), 2540–2553. https://doi.org/10.1111/gcb.12879

Kanda, N., Leary, R.F. & Allendorf, F.W. (2002). Evidence of introgressive hybridization between bull trout and brook trout. *Transactions of the American Fisheries Society*, 131(4), 772–782. https://doi.org/10.1577/1548-8659(2002)131%3C0772:EOIHBB%3E2.0.CO;2

Karas, N. (2015). *Brook trout: A thorough look at North America's great native trout, its history, biology, and angling possibilities*, Revised edition. New York, NY: Skyhorse Publishing.

La Sorte, F.A. & Thompson, F.R., III (2007). Poleward shifts in winter ranges of North American birds. *Ecology*, 88(7), 1803–1812. https://doi.org/10.1890/06-1072.1

Leary, R.F., Allendorf, F.W. & Forbes, S.H. (1993). Conservation genetics of bull trout in the Columbia and Klamath river drainages. *Conservation Biology*, 7(4), 856–865. https://doi.org/10.1046/j.1523-1739.1993.740856.x

Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884), 1768–1771. https://doi.org/10.1126/science.1156831

Leppi, J.C., Rinella, D.J., Wilson, R.R. & Loya, W.M. (2014). Linking climate change projections for an Alaskan watershed to future coho salmon production. *Global Change Biology*, 20(6), 1808–1820. https://doi.org/10.1111/gcb.12492

Luce, C., Staab, B., Kramer, M., Wenger, S., Isaak, D. & McConnell, C. (2014). Sensitivity of summer stream temperatures to climate variability in the Pacific Northwest. *Water Resources Research*, 50(4), 3428–3443. https://doi.org/10.1002/2013wr014329

Maire, A., Thierry, E., Viechtbauer, W. & Daufresne, M. (2019). Poleward shift in large-river fish communities detected with a novel meta-analysis framework. *Freshwater Biology*, 64(6), 1143–1156. https://doi.org/10.1111/fwb.13291

Mantua, N., Tohver, I. & Hamlet, A. (2010). Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climatic Change*, 102(1), 187–223. https://doi.org/10.1007/s10584-010-9845-2

Olden, J.D., Kennard, M.J., Lawler, J.J. & Poff, N.L. (2011). Challenges and opportunities in implementing managed relocation for conservation of freshwater species. *Conservation Biology*, 25(1), 40–47. https://doi.org/10.1111/j.1523-1739.2010.01557.x

Palmer, M.A., Lettenmaier, D.P., Poff, N.L., Postel, S.L., Richter, B. & Warner, R. (2009). Climate change and river ecosystems: Protection and adaptation options. *Environmental Management*, 44(6), 1053–1068. https://doi.org/10.1007/s00267-009-9329-1

Palmer, M.A., Liermann, C.A.R., Nilsson, C., Flörke, M., Alcamo, J., Lake, P.S. et al. (2008). Climate change and the world's river basins: Anticipating management options. *Frontiers in Ecology and the Environment*, 6(2), 81–89. https://doi.org/10.1890/060148

Petersen, J.H. & Kitchell, J.F. (2001). Climate regimes and water temperature changes in the Columbia River: Bioenergetic implications for predators of juvenile salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(9), 1831–1841. https://doi.org/10.1139/f01-111

Pound, K.L., Larson, C.A. & Passy, S.I. (2021). Current distributions and future climate-driven changes in diatoms, insects and fish in U.S. streams. *Global Ecology and Biogeography*, 30(1), 63–78. https://doi.org/10.1111/geb.13193

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J. et al. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3), 849–873. https://doi.org/10.1111/brv.12480

Ruesch, A.S., Torgersen, C.E., Lawler, J.J., Olden, J.D., Peterson, E.E., Volk, C.J. et al. (2012). Projected climate-induced habitat loss for salmonids in the John Day River network, Oregon, U.S.A. *Conservation Biology*, 26(5), 873–882. https://doi.org/10.1111/j.1523-1739.2012.01897.x

Stockwell, D.R.B. & Peterson, A.T. (2002). Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, 148(1), 1–13. https://doi.org/10.1016/s0304-3800(01)00388-x

Su, G., Logez, M., Xu, J., Tao, S., Villéger, S. & Brosse, S. (2021). Human impacts on global freshwater fish biodiversity. *Science*, 371(6531), 835–838. https://doi.org/10.1126/science.abd3369

Swets, J. (1988). Measuring the accuracy of diagnostic systems. *Science*, 240(4857), 1285–1293. https://doi.org/10.1126/science.3287615

Taniguchi, Y., Rahel, F.J., Novinger, D.C. & Gerow, K.G. (2011). Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(8), 1894–1901. https://doi.org/10.1139/f98-072

Thuiller, W., Georges, D., Engler, R. & Breiner, F. (2020). biomod2: Ensemble platform for species distribution modeling. R package version 3.3-7.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009). BIOMOD — A platform for ensemble forecasting of species distributions. *Ecography*, 32(3), 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E. et al. (2020). Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *Bioscience*, 70(4), 330–342. https://doi.org/10.1093/biosci/biaa002

Trenberth, K. (2011). Changes in precipitation with climate change. *Climate Research*, 47(1), 123–138. https://doi.org/10.3354/cr00953

Van Zuiden, T.M., Chen, M.M., Stefanoff, S., Lopez, L. & Sharma, S. (2016). Projected impacts of climate change on three freshwater fishes and potential novel competitive interactions. *Diversity and Distributions*, 22(5), 603–614. https://doi.org/10.1111/ddi.12422

van Vliet, M.T., Franssen, W.H., Yearsley, J.R., Ludwig, F., Haddeland, I., Lettenmaier, D.P. et al. (2013). Global river discharge and water temperature under climate change. *Global Environmental Change*, 23(2), 450–464. https://doi.org/10.1016/j.gloenvcha.2012.11.002

van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K. et al. (2011). The representative concentration pathways: An overview. *Climatic Change*, 109(1), 5–31. https://doi.org/10.1007/s10584-011-0148-z

Waldock, C., Dornelas, M. & Bates, A.E. (2018). Temperature-driven biodiversity change: Disentangling space and time. *Bioscience*, 68(11), 873–884. https://doi.org/10.1093/biosci/biy096

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J. C. et al. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389–395. https://doi.org/10.1038/416389a

Wang, C.J., Schaller, H.A., Coates, K.C., Hayes, M.C. & Rose, R.K. (2020). Climate change vulnerability assessment for Pacific lamprey in rivers of the western United States. *Journal of Freshwater Ecology*, 35(1), 29–55. https://doi.org/10.1080/02705060.2019.1706652

Weber, N., Bouwes, N., Pollock, M.M., Volk, C., Wheaton, J.M., Wathen, G. et al. (2017). Alteration of stream temperature by natural and artificial beaver dams. *PLoS ONE*, 12(5), e0176313. https://doi.org/10.1371/journal.pone.0176313

Wenger, S.J., Isaak, D.J., Luce, C.H., Neville, H.M., Fausch, K.D., Dunham, J.B. et al. (2011). Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences*, 108(34), 14175–14180. https://doi.org/10.1073/pnas.1103097108

Wenger, S.J. & Olden, J.D. (2012). Assessing transferability of ecological models: An underappreciated aspect of statistical validation. *Methods in Ecology and Evolution*, 3(2), 260–267. https://doi.org/10.1111/j.2041-210x.2011.00170.x

Williams, J.E., Williams, R.N., Thurow, R.F., Elwell, L., Philipp, D.P., Harris, F.A. et al. (2011). Native fish conservation areas: A vision for large-scale conservation of native fish communities. *Fisheries*, 36(6), 267–277. https://doi.org/10.1080/03632415.2011.582398

Winter, M., Fiedler, W., Hochachka, W.M., Koehncke, A., Meiri, S. & Riva, I.D. (2016). Patterns and biases in climate change research on amphibians and reptiles: A systematic review. *Royal Society Open Science*, 3(9), 160158. https://doi.org/10.1098/rsos.160158

Zanden, M.J.V., Casselman, J.M. & Rasmussen, J.B. (1999). Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, 401(6752), 464–467. https://doi.org/10.1038/46762

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