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Drivers and uncertainties of forecasted range shifts for warm-water fishes under climate and land cover change

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Abstract

Land cover is an important determinant of aquatic habitat and is projected to shift with climate changes, yet climate-driven land cover changes are rarely factored into climate assessments. To quantify impacts and uncertainty of coupled climate and land cover change on warm-water fish species' distributions, we used an ensemble model approach to project distributions of 14 species. For each species, current range projections were compared to 27 scenario-based projections and aggregated to visualize uncertainty. Multiple regression and model selection techniques were used to identify drivers of range change. Novel, or no-analogue, climates were assessed to evaluate transferability of models. Changes in total probability of occurrence ranged widely across species, from a 63% increase to a 65% decrease. Distributional gains and losses were largely driven by temperature and flow variables and underscore the importance of habitat heterogeneity and connectivity to facilitate adaptation to changing conditions. Finally, novel climate conditions were driven by mean annual maximum temperature, which stresses the importance of understanding the role of temperature on fish physiology and the role of temperature-mitigating management practices.

Introduction

Changes in climate, a dominant control over the natural distribution of species, has and will continue to cause many species to shift their geographic range (Walther 2002; Parmesan and Yohe 2003; Staudinger et al. 2013). Freshwater systems in particular are highly susceptible to direct and indirect impacts of climate change (Sala et al. 2000; Heino et al. 2009). Directly, changes in climate patterns influence temperature and precipitation regimes, which affect thermal and hydraulic conditions within a river (Kernan et al. 2010; Figure 1). Changes to temperature-dependent processes, such as growth and survival of fishes, will likely vary by thermal guild (i.e., cold-water, cool-water, warm-water; (Magnuson et al. 1979). Sensitivity of cold-water fish distributions, particularly salmonids, to climate changes has been the focus of many scientific investigations (Comte et al. 2013). Although less studied, distributions of warm-water fishes have been associated with temperature (Meisner et al. 1987; Buisson et al. 2008), and are generally expected to benefit from climate change through range expansions. Observations of warm-water fish range expansions have been made in the Upper Rhône River in France (Daufresne et al. 2004), and the expansion of northern boundaries of fish species ranges has occurred in Ontario lakes (Alofs et al. 2014). Additionally, species distribution models have projected range expansions for warm-water fish species in Wisconsin (Lyons et al. 2010) and Germany (Markovic et al. 2012), given populations can overcome physical and ecological barriers.

As climate patterns shift, land cover, a well-known determinant of aquatic habitat, water quality and biotic communities (Allen 2004), will also shift. For example, climate change scenarios project winter wheat and cotton production to expand northward, the distribution of grassland to expand across the Great Plains, row-crop production to expand northward, and the

distribution of forest to expand in the south (Lant et al. 2016). Interactive effects of climate and land cover changes will undoubtedly influence reach-scale temperature and flow regimes, and site-scale substrate and physiochemical properties (Figure 1). These effects influence habitat conditions that contribute to distributional patterns of fishes (Wang et al. 1997; Lammert and Allan 1999; Allan 2004). While climate change assessments often assume land cover to be static over time (Leathwick et al. 2008; Lyons et al. 2010; Bond et al. 2011), recent efforts have begun to evaluate combined climate and land cover impacts on aquatic habitat and macroinvertebrate distributions (Herb et al. 2014; Mantyka-Pringle et al. 2014; Kuemmerlen et al. 2015). Climate-driven land cover changes may complicate the general expectation of warm-water fishes to expand distributional ranges with climate change, though these indirect effects of climate change have not yet been investigated.

Our objectives were to 1) evaluate range shifts of 14 warm-water fish species native to the Central United States in response to coupled climate and land cover scenarios, 2) identify the major drivers of range gain and range loss, and 3) assess transferability of models to future climate scenarios. We hypothesize that warm-water species will generally be projected to have range expansions, as climate variables were most influential in model development across species (Bouska et al. 2015). Finally, we hypothesize that novel climates will appear in the southern extent of our study area as temperatures increase under climate scenarios, limiting the transferability of models to this region.

Materials and methods

Climate and land cover scenarios

Climate variables used to model the current range of fish distributions were obtained through the National Climate Data Center (<http://www.ncdc.noaa.gov/>). Climate variables included mean annual maximum and minimum air temperature, and mean seasonal and annual precipitation and were represented by 10-year averages (Table 1). Climate scenarios were used to assess the impacts of future climates on fish species' distributions. Three different greenhouse gas emissions trajectories (representative concentration pathways [RCPs]), were used as the basis for future scenarios, including the 2.6 (low emissions), 4.5 (medium-low emissions) and 8.5 (high emissions) Watts/m² RCPs (IPCC 2013). Three general circulation models (GCMs) were selected based on two criteria: 1) high performance in hindcasting climate variables for the study area (Sheffield et al. 2013), and 2) to encompass the full range of variability across future climate projections from all available GCMs (Knutti et al. 2013; Maloney et al. 2014). The GCMs selected included IPSL-CM5A (Institut Pierre-Simon Laplace), MRI-CGCM3 (Meteorological Research Institute), and NOR-ESM (Norwegian Climate Centre). The scenario-based climate data were downloaded from the Coupled Model Intercomparison Project (CMIP5), and downscaled for the study area through the use of weather generator techniques to provide monthly and annual air temperature and precipitation data for the years 2006 through 2099 (Schoof et al. 2007; Schoof 2015). Three time periods were used in our scenarios: 2030-2039, 2060-2069, and 2090-2099. Climate variables were averaged across each time period.

Discharge data from USGS gages (<http://waterdata.usgs.gov/nwis>) was used to develop regression models from which discharge at ungaged stream segments was estimated for current conditions and all climate change scenarios (Bouska 2014; Table 1). Discharge variables included the 50th and 90th percentile of flow, and a flow variability index (90th/10th percentile).

Land cover variables for current conditions included rowcrops (corn, soybean, and cotton), wheat, forest, and developed land and derived from the National Agricultural Statistics Service's Cropland Data Layer (<http://nassgeodata.gmu.edu/CropSpace/>). For the identified climate change scenarios, multivariable fractional polynomials were applied in a logistic regression context to model land cover variables as a response to climatic, edaphic, and topographic determinants (Stoebner and Lant 2014; Lant et al. 2016). Developed land and water classifications were not modeled and therefore assumed to not change under any scenario. Each land cover projection produced a probability of occurrence of the land cover for each pixel in the study area, which was used to calculate a percent within each of the 1,085 12-digit hydrologic unit codes (HUC). All stream segments within a HUC were attributed the same land cover percentages.

Twelve static variables, meaning no change between the current conditions and climate change scenarios, were used to model distributions. Static variables included nine geological variables derived from the USGS Surficial Geology by Major River Basins dataset (http://water.usgs.gov/GIS/metadata/usgswrd/XML/mrb_e2rf1_sgeol.xml) and three physical variables (i.e., elevation, drainage area, and slope) that originated from the National Hydrography Dataset Plus (<http://www.horizon-systems.com/nhdplus/>).

Species distribution models

Projections of fish species distributions under climate and land cover change scenarios were modeled using previously developed and evaluated species distribution models for 14 warm-water fish species native to the Central United States: bigeye shiner (*Notropis boops*), bigmouth shiner (*Hybopsis dorsalis*), freckled madtom (*Noturus nocturnus*), largescale

stoneroller (*Campostoma oligolepis*), orangespotted sunfish (*Lepomis humilis*), orangethroat darter (*Etheostoma spectabile*), plains minnow (*Hybognathus placitus*), plains topminnow (*Fundulus sciadicus*), river carpsucker (*Carpionodes carpio*), shortnose gar (*Lepisosteus platostomus*), slenderhead darter (*Percina phoxocephala*), slender madtom (*Noturus exilis*), smallmouth bass (*Micropterus dolomieu*), and suckermouth minnow (*Phenacobius mirabilis*). Species were selected based on whether 1) the study area encompassed the species' full native ranges, 2) species presence observations were representative of its full native range, and 3) sufficient presence observations (>30) were collected. Fish data used to develop and validate the models originated from state natural resource agencies from ten states representing the central United States (Arkansas, Illinois, Iowa, Kansas, Louisiana, Minnesota, Missouri, Nebraska, North Dakota, and Wisconsin; Figure 2). Although each state has different stream sampling protocols, all fish data used for this study were collected between 2000 and 2010 and originated from representative stream sampling.

Ensemble models were developed from generalized linear models, generalized boosted regression models, classification tree analysis, random forest models, and multi-adaptive regression splines using the BIOMOD2 package in R to relate fish presence/absence data with environmental data (Thuiller et al. 2009). The ensemble models were used to determine 'current' distributions of fish species at the stream segment scale using 2011 values of environmental data, and project future distributions using scenario-based environmental data (Table 1). No site-level environmental data collected at the time of fish sampling were used in modeling fish distributions due to differences in stream sampling protocols. Additional details of the modeling methodology can be found in Bouska et al. 2015.

Data analysis

To assess changes in fish distribution size and spatial changes in fish distribution based on the probability of occurrence, two statistics were calculated for each scenario. These statistics only included stream segments with a probability of occurrence that exceeded the threshold of occurrence, identified in the validation stage of model development (Bouska et al. 2015). In other words, the calculated statistics only included stream segments at which the occurrence of a species was positive. The percent change in total probability of occurrence for each species was calculated by summing occurrence probabilities and calculating the percent change from the current projected distribution. Similarly, the percent change in mean probability of occurrence was calculated by first taking the absolute value of the difference between the current projected mean probability of occurrence and each scenario mean probability of occurrence and calculating the percent change from current projected distribution.

Consensus indices were developed for each species to visualize range change uncertainty across all scenarios. First, the probabilities of the three GCM projections for each scenario were averaged, producing a single probability for each RCP-x-time period combination per species. The resulting nine consensus projections were then combined in a single map to visualize agreement across scenarios of range maintained, gained, and lost for each species.

To identify the major drivers of range shifts, we created five candidate multiple regression models for each species from climate and land cover variables that were hypothesized to influence range change. Models were used to predict average change in probability of occurrence of individual species across all 27 scenarios, separately for range gain and range loss as those may be driven by different processes. Four candidate models were developed separately for temperature, precipitation, discharge, and land cover variables across the study area, using

the average change in these variables across all scenarios. The fifth candidate model included all climate and land use variables. Akaike Information Criteria (AIC) was used to select among candidate regression models to assess the likelihood of each model in explaining change in probability of occurrence. Only variables used in individual species' distribution models were included in the respective regression models. Land cover change variables were log transformed [$\log_{10}(x+100)$] to meet normality assumptions. Multiple regression and AIC analyses were conducted using R (R Core Team 2014) .

The extrapolation detection (ExDet) tool was used to identify where scenarios relied upon climate variables that were outside the range of individual variables used to model current distributions (hereafter referred to as type 1 novelty) as well as new combinations of variables within univariate range, or type 2 novelty (Mesgaran et al. 2014). This method utilizes the Mahalanobis distance metric (Mahalanobis 1936), which measures similarity between current and scenario climate variables by considering deviations from the mean and correlations between variables (Mesgaran et al. 2014). We evaluate novelty and associated drivers for each scenario using six climate variables (mean annual maximum and minimum temperature, total annual, summer, spring, and winter precipitation) to inform where and why climate projections may be less reliable. The ExDet tool was used for all extrapolation analyses (<http://www.climond.org/exdet>).

Results

We projected both range expansions and contractions of suitable conditions for warm-water fish species under future climate change. Percent change in total probability of occurrence increased for plains minnow (range: 29 – 63%), orangethroat darter (11 – 46%), suckermouth

minnow (-8 – 40%), orangespotted sunfish (6 – 21%), and river carpsucker (6 – 18%; Figure 3A). In contrast, bigmouth shiner (-60 – -31%), slender madtom (-47 – -38%), bigeye shiner (-65 – -11%), freckled madtom (-43 – -20%), and slenderhead darter (-38 – -8%) had negative percent change in total probability of occurrence, indicating lower overall probabilities of occurrence under climate change scenarios. Shortnose gar (8%), largescale stoneroller (8%), plains minnow (10%), and plains topminnow (15%) had the lowest percent mean change in probability of occurrence and thus the least amount of spatial range shift (Figure 3B). Percent mean change in probabilities of occurrence indicated spatial range shifts and were highest for bigmouth shiner (mean = 55.8%), slender madtom (47%), smallmouth bass (47%), freckled madtom (45%), and orangethroat darter (30%).

Consensus projections across scenarios indicate that conditions associated with the presence of orangethroat darter, river carpsucker, suckermouth minnow, and plains minnow are likely to expand northward, regardless of scenario (Figures 4 and 5). Other species, including slenderhead darter, largescale stoneroller, and shortnose gar, showed loss of their northern range, regardless of scenario. Bigeye shiner, bigmouth shiner, slender madtom, and freckled madtom exhibited almost complete or significant loss of current range regardless of scenario. River carpsucker, suckermouth minnow, slenderhead darter, and shortnose gar showed suitable conditions to expand into relatively higher elevations of south-central Missouri and northwestern Arkansas. The central range of suitable conditions for smallmouth bass generally disappeared in all scenarios, while the range in the Ozarks was maintained and range gain occurred in parts of Minnesota, eastern Wisconsin and eastern North Dakota.

The candidate model with all climate and land use variables had the greatest explanatory power of species range gain and loss for all species, in comparison to the temperature,

precipitation, discharge or land use models (Tables 2 and 3). For five of the nine species that exhibited species loss, temperature was the dominant driver of range loss. Range loss of freckled madtom, slender madtom, and largescale stoneroller was best explained by changes in discharge variables while slenderhead darter was best explained by land cover changes. Of the eleven species that exhibited range gains, six were best explained by temperature variables, four by discharge variables, and one by precipitation variables (Table 3).

Novel climates emerged from the selected climate scenarios as type 1 novelty, meaning conditions are novel because they are outside the range of individual covariates (Figure 6, Supplementary material). Nearly every scenario had novel climate emerging in Louisiana, Arkansas, and Kansas. As scenarios advanced in time and RCP, novel climates encompassed more of the study area and generally advanced from the southwest towards the northeastern portion of the study area. The only portion of the study area that did not change to a novel climate under any single scenario were northeast Iowa, eastern Minnesota, and Wisconsin (S3 and S4). The drivers of novel climates for different scenarios were identified by the extrapolation detection tool as primarily mean annual maximum temperature, followed by mean annual minimum temperature and annual precipitation.

Discussion

Our results of climate and land use projections suggest that some warm-water fishes are expected to benefit from future climate changes through expansion of suitable conditions, but others may not. In fact, some warm-water species are projected to undergo substantial losses in range. Five of the fourteen species modeled are projected to expand northward while maintaining the majority of their current distribution. Another three species are projected to expand range

northward while experiencing range contraction in the southern extent of their current distributions. Of the eight species with potential northward range expansion, both range losses and gains are predominantly driven by temperature. Three species are projected to contract the northern extent of their range and experience a slight expansion in their southern extent. The three remaining species are projected to lose the majority of their current range without substantial gains elsewhere. Of the six species projected to lose northern portions of their range or their complete range, range losses and gains are driven by different candidate models, suggesting distribution sensitivity to changes in precipitation, discharge, land cover, as well as temperature. A review of known life history traits and strategies for these species reveals no strong associations with range changes or drivers of range change.

Few of our selected species have been modeled elsewhere, limiting our ability to compare our results to those of other studies; however, smallmouth bass distribution has been modeled extensively at both small and large scales. Comparison of our smallmouth bass projections with efforts to model the northern range of the species shows our models predict greater range gains in Minnesota and Wisconsin (Stewart et al. 2016). However, large-scale models of lake-dwelling smallmouth bass predict expansion of its northern range into Canada (Sharma et al. 2007) and most of the continental U.S. (Sharma and Jackson 2008). Similarly, models for stream-dwelling smallmouth bass forecast expansion of this species' range throughout Wisconsin (Lyons et al. 2010), the Muskegon River Watershed in Michigan (Steen et al. 2010), and the John Day River in Oregon (Lawrence et al. 2014). In the central portion of smallmouth bass' range, our projections show a consistent loss of smallmouth bass occurrence under coupled climate and land cover change scenarios. Similarly, an age-structured model for the Kankakee River in Illinois suggested climate change reduced smallmouth bass abundance by 69%, with further

simulations suggesting historic land cover conditions may be able to mitigate negative climate change impacts (Peterson and Kwak 1999).

We determined temperature and discharge to be the dominant drivers of both range gain and loss across the 14 species modeled. Given the high sensitivity of the distribution models to climate variables relative to land cover variables (Bouska et al. 2015), we expected temperature, precipitation and discharge variables to also be primary drivers of distributions under climate change scenarios despite significant changes in land cover (Lant et al. 2016). In rivers and streams in France, modeled changes in temperature seasonality were the primary driver of fish species colonizations, while both temperature and precipitation changes were important in distributional declines (Conti et al. 2015). Changes in water temperature, discharge, and ocean currents have been identified as primary drivers of distributional change in Australian fishes (Booth et al. 2011). From a management perspective, conservation of native warm-water fishes in the face of climate change will require thermal and flow refugia within stream and river environments. In the Midwest, where a large number of streams have been channelized (Mattingly et al. 1993), and in the Great Plains, where streams are highly fragmented (Perkin et al. 2015), maintaining and restoring habitat heterogeneity and connectivity throughout the river network may be critical to provide thermal and flow refugia.

Distilling information across climate and land cover scenarios is important given uncertainties in the trajectory of climate change. Recently, consensus projections have been used to disentangle the uncertainty by aggregating projections to provide maps of agreement and disagreement (i.e., variability between projections) across scenarios (Forester et al. 2013). Locations where a species is ‘maintained’ throughout all scenarios may indicate areas where populations are expected to be stable, while locations where all scenarios agree there is a gain

can be considered opportunities, and locations where all scenarios agree there is loss could be perceived as most vulnerable. Therefore, consensus projections can aid natural resource agencies in conservation planning by providing a clearer picture of a species' spatiotemporal vulnerabilities.

Another form of uncertainty when using species distribution models to make projections lies in model transferability. Projections made under novel climatic conditions are less reliable (Elith et al. 2010) because they are outside the range of conditions used to develop the model (Fitzpatrick and Hargrove 2009). Our results show novel climates encompassed an increasing amount of the study area both as greenhouse gas emission scenarios increased and with time. We expected the southern portion of the study area to have novel conditions under climate scenarios due to increasing temperatures, but had not anticipated the wide extent across the study area that was considered to have novel climate under more extreme climate scenarios. These results suggest that model projections for earlier time periods and for lower emissions are more reliable than those projections further out in time and with greater emissions.

Model limitations

Although the scenario projections suggest some species increase in range while others decrease in range under climate change scenarios, these results are contingent on models capturing complete response curves to environmental variables. Where response curves are not fully captured, projections may overestimate range gains and underestimate range losses. For example, four of the five species projected to have significant range expansion (orangethroat darter, plains minnow, river carpsucker, and suckermouth minnow) had no upper thermal limit estimated in the underlying model's response curves. Therefore, annual mean maximum

temperature did not result in range losses for these species, yet in reality an upper thermal limit influences physiological functions, oxygen availability and toxicity of pollutants (Ficke et al. 2007). Annual mean maximum temperature was identified as the major driver of novel climate under nearly all scenarios, increasing the importance of understanding thermal tolerance limits. Efforts to identify thermal tolerances and incorporate environmental gradients that exceed the upper and lower limits of the species occurrence would improve the predictive capacity of SDMs (Austin 2007). Sub-lethal effects of temperature resulting from prolonged exposure to sub-optimal thermal conditions can contribute to reduced fitness and should also be considered (Whitney et al. 2016). Further, indirect effects of temperature include food web changes, which may alter food availability and biotic interactions that ultimately affect distributions (Portner and Farrell 2008).

Environmental predictor variables used in this analysis could be improved with additional in-stream and site-level data. The limited role of land cover effects on fish distribution changes may be a result of modeling responses to a driver of stress (i.e., land cover) as opposed to metrics of the actual stress (i.e., substrate, dissolved oxygen). Use of finer-scale environmental variables may reveal our results here underestimate the role of land cover on fish distributions, but would require additional site-level data to be collected in a standardized fashion across states. Scenarios that incorporate effects of climate on developed land would improve model predictions in areas likely to undergo development. We used mean annual minimum and maximum air temperatures in our models due to limited water temperature data. Although air and water temperatures are highly correlated (Stefan and Preud'homme 1993), factors such as riparian shading, snowmelt, and groundwater inputs influence local water temperatures and can influence species' distributions, growth and abundance (Poole and Berman 2001; Rutherford et al. 2004; Whitley

et al. 2006; Brewer 2013; Westhoff and Paukert 2014). For example, Westhoff and Paukert (2014) found stream temperatures could be 10° C different over short distances due to groundwater influences. Further, use of stream water temperature could allow the evaluation of increased riparian vegetation as a management tool to reduce climate-induced increases in mean stream temperatures and water temperature fluctuations. Discharge estimates could also be improved to account for dams, groundwater inputs, and evapotranspiration that influence hydrology and vary throughout our study area (Dunn and Mackay 1995).

Adaptability of species and populations to climate and land cover change will likely depend upon ecological traits. For example, organisms with larger bodies and specialized diets may be vulnerable to climate change (Lurgi et al. 2012). Further, those species with limited ranges, low growth and fecundity rates, and/or delayed maturation are expected to be less tolerant of environmental change (Olden et al. 2011). Our models are limited in that they do not account for adaptive capacity to environmental change. To do so would require knowledge of a species' ability to tolerate environmental change via phenotypic plasticity, evolution, or dispersal (Ficke et al. 2007). Some species can adapt to environmental change by shifting life history traits over short timespans (Reznick and Ghalambor 2005). Species with periodic and equilibrium life history strategies may need to adapt life history traits in order to persist as they depend on predictable seasonal changes and stable environments, respectively (Winemiller and Rose 1992). Opportunistic species on the other hand may find the changes in the environment are optimal for their proliferation. For example, if climate change produces a more dynamic environment with increased disturbances, opportunistic species may thrive without adapting life history traits because they generally respond positively in unpredictable environments (Winemiller 2005). Finally, in this modeling exercise, a species is modeled as a single unit, when in reality many

species exist as multiple populations, each with their own range of tolerances, and exist in multiple assemblages with varying interactions. While accounting for these factors would improve model projections, it would require a knowledge base of environmental tolerances and how they vary within a species; for warm-water, non-game stream fishes, there are currently limited data at this level of detail.

Our results highlighted that warm-water species will likely exhibit a wide range of responses to coupled climate and land cover change, from significant expansion of suitable conditions to significant contractions, with varying degrees of certainty. Distributional gains and losses were largely driven by temperature and discharge variables and underscore the importance of habitat heterogeneity and connectivity in facilitating adaptation to changing conditions. Finally, novel climate conditions were driven by mean annual maximum temperature, which stresses the importance of understanding the role of temperature on fish physiology and the role of temperature-mitigating management practices.

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182 American fishes: implications for population regulation. *Canadian Journal of Fisheries*
183 *and Aquatic Science* **49**:2196-2218.
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186 Table 1. A list of variables included in model development. Climate and land cover variables
 187 differed between current distribution model and scenario-based models while physical variables
 188 were fixed.

Variable type	Variable	Current model source	Scenario source
Climate	Annual mean minimum temperature	National Climate Data Center	Coupled Model Intercomparison Project (CMIP5), downscaled as described by Schoof 2015 and Schoof et al. 2007
	Annual mean maximum temperature		
	Total annual precipitation		
	Total spring precipitation		
	Total summer precipitation		
	Total winter precipitation		
Discharge	Discharge (50 th percentile)	=(0.840*drainage area) – (0.191*mean annual maximum temperature) + (0.003*mean annual total precipitation) + 1.307 (Bouska 2014)	
	Discharge (90 th percentile)	=(0.820*drainage area) – (0.180*mean annual maximum temperature) + (0.004*mean annual total precipitation) + 2.371 (Bouska 2014)	
	Flow variability	= Discharge 90 th /Discharge 10 th	
Land cover	Rowcrops	National Agricultural Statistics Service’s Cropland Data Layer	Stoebner 2016; Lant et al. 2016
	Wheat		
	Forest		
	Grassland		
	Developed	National Agricultural Statistics Service’s Cropland Data Layer	
Physical	Red clay	USGS Surficial Geology by Major River Basins dataset	
	Alluvium		
	Sand/silt residuum		
	Sand/stone colluvium		

	Loess	
	Till moraine gravel	
	Pre-Wisconsin deposits	
	Sand sheets	
	Ice-laid deposits	
	Elevation	National Hydrography Dataset Plus
	Drainage area	
	Slope	

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Table 2. Comparison of multiple regression models for range loss of each species using adjusted R^2 and Akaike Information Criterion (AIC). Bolded values indicate models with greatest explanatory power. Species not included had too few occurrences of range loss to analyze. Adjusted R^2 values less than 0.001 are noted as ~0.

Species	Temperature model		Precipitation model		Discharge model		Land cover model		All variable model	
	Adj. R^2	Δ AIC	Adj. R^2	Δ AIC	Adj. R^2	Δ AIC	Adj. R^2	Δ AIC	Adj. R^2	Δ AIC
Bigeye shiner	0.08	2790	0.01	5135	0.07	3220	0.03	4487	0.15	0
Bigmouth shiner	0.15	3611	0.04	21181	0.01	25461	0.01	24676	0.18	0
Freckled madtom	0.08	54897	0.17	43051	0.31	19770	0.01	64096	0.42	0
Largescale stoneroller	0.10	4218			0.17	2051	0.001	6804	0.23	0
Plains topminnow	0.08	448	0.07	672	0.04	1037	0.02	1342	0.11	0
Shortnose gar	0.10	1746	0.06	2704	0.07	2329	0.04	3098	0.17	0
Slenderhead darter	0.03	5347	0.01	6609	~0	7155	0.03	4946	0.10	0
Slender madtom	0.05	13786	0.01	21059	0.06	10871	0.002	21702	0.12	0
Smallmouth bass	0.25	3873	0.02	12367	0.06	10987	0.05	11545	0.34	0

Table 3. Comparison of multiple regression models for range gain of each species using adjusted R^2 and Akaike Information Criterion (AIC). Bolded values indicate models with greatest explanatory power. Species without values had too few occurrences of range gain to analyze. Adjusted R^2 values less than 0.001 are noted as ~0.

Species	Temperature model		Precipitation model		Discharge model		Land cover model		All variable model	
	Adj. R^2	Δ AIC	Adj. R^2	Δ AIC	Adj. R^2	Δ AIC	Adj. R^2	Δ AIC	Adj. R^2	Δ AIC
Bigmouth shiner	0.14	1048	0.05	2093	0.008	2582	0.02	2496	0.22	0
Largescale stoneroller	0.08	1094			0.10	891	0.02	2049	0.15	0
Orangespotted sunfish	0.001	9	~0	85	~0	57	~0	113	0.001	0
Orangethroat darter	0.21	37625	0.10	54325	0.004	68292	0.07	58863	0.40	0
Plains minnow	0.23	2083	0.01	3875	0.14	1583	0.08	2727	0.32	0
Plains topminnow	0.11	2351	0.04	3380	0.005	3861	0.004	3866	0.25	0
River carpsucker	0.05	9	~0	6782	0.001	6599	~0	6775	0.05	0
Shortnose gar	0.03	2156	0.06	1601	0.09	1049	0.01	2350	0.14	0
Slenderhead darter	0.05	1208	0.10	604	~0	1927	0.01	1804	0.25	0
Smallmouth bass	0.32	3272	0.12	6730	0.37	2192	0.004	8489	0.47	0
Suckermouth minnow	0.01	9239	~0	10415	0.10	1552	0.02	8918	0.11	0

206 **Figure legends**

207 Figure 1. Aquatic habitats are subject to direct (e.g., temperature and precipitation) and indirect
208 (e.g., land cover changes) effects of climate change.

209 Figure 2. The study area used for both model development (Bouska et al. 2015) and scenario
210 analysis.

211 Figure 3. Percent change in total probability of occurrence (A) across all stream segments from
212 the current distribution, and percent change in mean probability of occurrence from the current
213 distribution across stream segments (B).

214 Figure 4. Consensus map of range change across climate and land cover scenarios for each
215 species. The projection is USA Contiguous Albers Equal Area Conic.

216 Figure 5. Consensus map of range change across climate and land cover scenarios for each
217 species. The projection is USA Contiguous Albers Equal Area Conic.

218 Figure 6. Novel climates, detected using the Extrapolation Detection Tool, for each of the
219 scenarios analyzed using the IPSL-CM5A.

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