Climate Change and Mountaintop-Removal Mining: A MaxEnt Assessment of the Potential Threat to West Virginian Fishes

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Abstract - Accounts of species' range shifts in response to climate change are rapidly accumulating. These range shifts are often attributed to species tracking their thermal niches as temperatures in their native ranges increase. Our objective was to estimate the degree to which shifts in water temperature driven by climate change may increase the exposure of West Virginia's native freshwater fishes to mountaintop-removal surface coal mining. We projected midcentury shifts in habitat suitability for 9 non-game West Virginian fishes via maximum entropy species distribution modeling, using a combination of physical habitat, historical climate conditions, and future climate data. Modeling projections for a high-emissions scenario (Representative Concentration Pathway 8.5) predict that habitat suitability will increase in high-elevation streams near mountaintop mining sites for 8 of 9 species, with increases in habitat suitability varying from 46% to 418%. We conclude that many West Virginian fishes will be at risk of increased exposure to mountaintop mining if climate change continues at a rapid pace.

Introduction

Quantifying and predicting species' responses to climate change is currently a high-priority research topic in biogeographical and conservation science (e.g., Angert et al. 2011, Lin et al. 2017, Pecl et al. 2017). In the Northern Hemisphere, species are responding by shifting their ranges to the north or to higher elevations (e.g., Chen et al. 2011, Chivers et al. 2017, Comte and Grenouillet 2013). These latitudinal and elevational range shifts may be a result of species tracking their thermal preferences as temperatures in their historical, native ranges increase (Comte et al. 2013, Freeman and Class Freeman 2014, Parmesan 2006). If so, range shifts should be most likely for vagile species that are physically capable of long-distance movements and for ectothermic species that have narrow thermal tolerances (Calosi et al. 2008, Deutsch et al. 2008).

Freshwater fishes of the Central Appalachian region in eastern North America may be particularly likely to shift to higher elevations in response to a warming climate. Like most primary freshwater fishes, they are obligate ectotherms that may encounter stressful or lethal conditions as ambient temperatures increase (see Farrell 2011). Furthermore, most major rivers in this region flow westward off of the Appalachian range to the Ohio River, which is also a predominantly westward

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flowing river that originates at the confluence of the Alleghany and Monongahela rivers, near Pittsburgh, PA (~42°N latitude), or they flow east to the Atlantic Ocean. Thus, the topography and elevation of the Appalachian range may provide opportunities for freshwater fishes to shift their ranges upslope, while latitudinal shifts that extend far north will not be feasible for many populations.

Unfortunately, fishes that shift to higher elevations in central Appalachia may be at risk of encountering another threat: increased exposure to mountaintop-removal (MTR) surface coal mining. Mountaintop-removal mining is pervasive throughout central Appalachia (Ferreri et al. 2004) and is particularly common in the state of West Virginia (Fig. 1). Damages to aquatic biota may occur through acute loss of headwater streams (via burial by valley fill) or chronic degradation of water quality and instream habitat further downstream (Bernhardt et al. 2012). Empirical reports of MTR impacts on native fishes take on various forms from the individual-level toxic effects of selenium, a common byproduct of MTR that causes teratogenic deformities (Lemly 1993, Palmer et al. 2010), to assemblage-level effects including decreased species richness and lower population densities (Hitt and Chambers

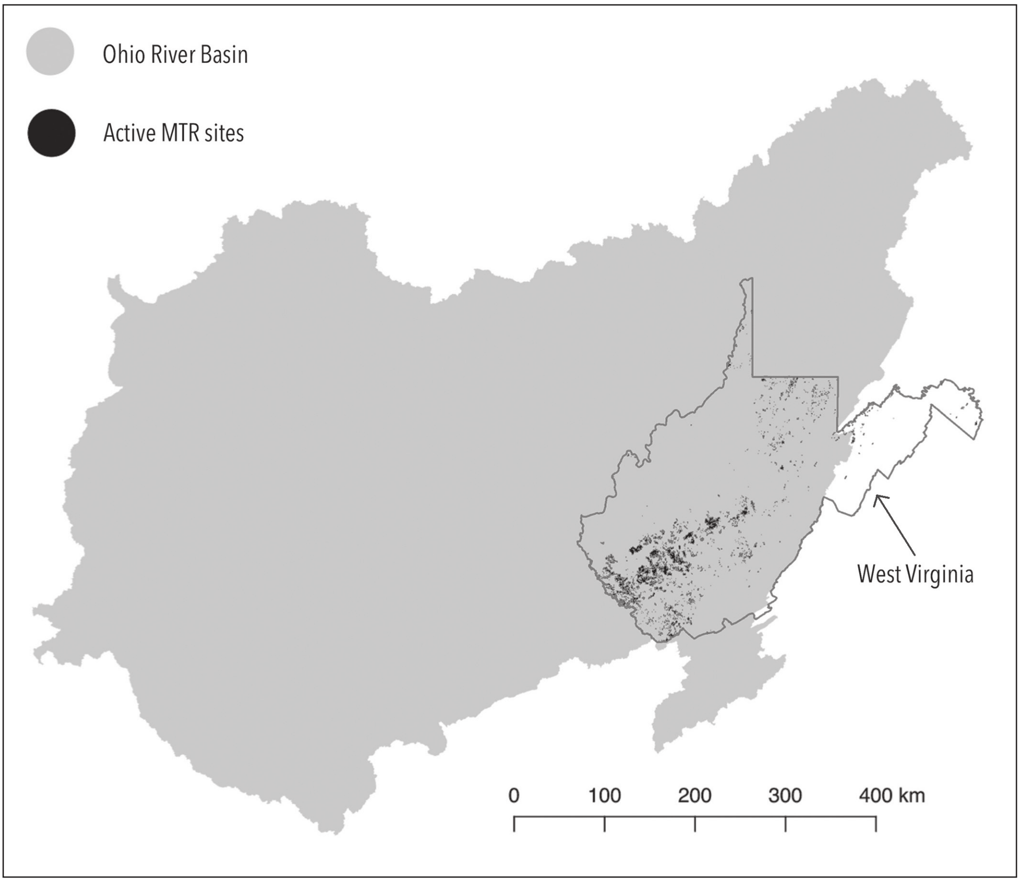

Figure 1. Map of the study site showing the Ohio River Basin (ORB; light gray), the state of West Virginia (outline), and the active mountaintop-removal (MTR; black) mining sites within West Virginia.

2014). Habitat models also suggest that MTR may have a negative effect on fish distributions, pushing them further downstream (Hopkins and Roush 2013).

In this study, we used maximum entropy (MaxEnt; Phillips et al. 2006) species distribution models (SDMs) to assess whether climate change and MTR may pose an interactive threat to the native fishes of West Virginia. This was a 2-stage process in which we first used physical habitat and historical climate data to build SDMs for a subset of the native fishes of West Virginia. We then predicted future habitat suitability under 2 midcentury climate-change scenarios. For each species and future climate scenario, we assessed changes in habitat suitability for streams in close proximity to MTR operations. However, our intent was not to model the effects of MTR on West Virginian fishes per se. Instead, we characterized the degree to which climate change may increase fish exposure to MTR via warming-induced upslope range shifts. Our analyses focused on a representative subset of non-game species. Other investigators have studied climate change and MTR effects on West Virginian game fishes, such as *Salvelinus fontinalis* (Mitchill) (Brook Trout; e.g., Ries and Perry 1995), but little is known about the potential consequences for the region's diverse non-game fishes.

Specific research objectives were to (1) build SDMs for a select subset of non-game fish species that are broadly representative of the native ichthyofauna of West Virginia, (2) predict changes in habitat suitability under 2 midcentury climate scenarios, and (3) use the projected habitat suitability maps to identify species that are likely to migrate to higher elevations, thereby increasing their exposure to MTR.

Methods

Fish species selection and occurrence data

We selected 9 non-game species for inclusion in our modeling study from the 176 documented native West Virginian fishes (Stauffer et al. 1995). Selection was guided by an iterative process. First, we removed species from the candidate list that did not have at least 200 occurrence records within the Ohio River Basin. We then sought to ensure that the selected species would be broadly representative of the autecological characteristics of all native West Virginian fishes in the Ohio River Basin (i.e., westward flowing rivers). To do so, we used a multivariate species-traits approach. We obtained species-level descriptions for 13 functional traits through an extensive literature review, as detailed in Woods and McGarvey (2018), then compiled them in a species × trait matrix. Traits included multiple indicators of body size (e.g., maximum total length, female length at maturation, mean egg diameter), maximum longevity, degree of parental care, adult habitat, vertical water-column position, adult feeding behavior, egg-deposition strategy, spawning season, and migratory behavior. We used the species × trait matrix to calculate pairwise Gower dissimilarities for all 136 native West Virginian fishes within the Ohio River Basin. Gower dissimilarity is commonly used in functional traits analysis because it is compatible with a combination of continuous (e.g., total length) and categorical (e.g., feeding behavior) variables (Gower 1971). Next, we conducted principal coordinates analysis to build a 2-dimensional trait-space ordination of the 136 fishes. Finally, we used the ordination plot to visually confirm that the selected fish species encompassed a large fraction of the total trait-space and were therefore representative of the overall range of West Virginian fish functional traits (Fig. 2).

We obtained presence-only occurrence records for each of the selected species from the spatially explicit Ichthymaps digital database (Frimpong et al. 2016). We included occurrence records distributed throughout the entire Ohio River Basin, the parent drainage to most rivers in West Virginia. Incorporating species' complete ranges throughout the Ohio River Basin, rather than truncated ranges within West Virginia, ensured that the MaxEnt background samples (see Species distribution models subsection below) would be representative of all habitats available to the modeled species (Elith et al. 2011, Yates et al. 2018). To account for potential spatial bias in the Ichthymaps occurrence records, we applied a spatial thinning algorithm to the occurrence data. Using the spThin package in R (Aiello-Lammens et al. 2015), we applied a nearest-neighbor search radius of 10 km to each Ichthymaps occurrence record. Fewer than 2% of all occurrence points were within 10 linear km of each other. We therefore concluded that geographic sampling bias was not a significant concern and retained all of the occurrence data in model development.

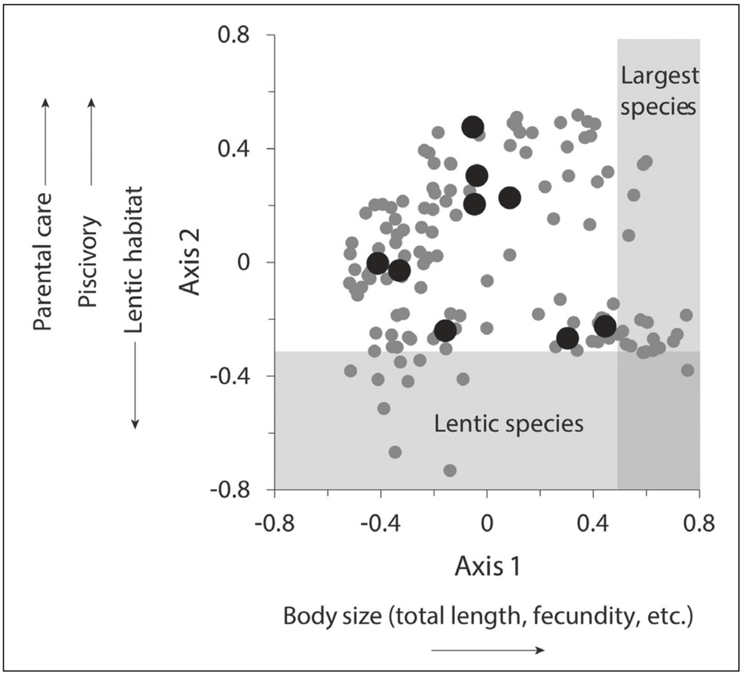

Figure 2. Ordination plot of the first 2 principal coordinate axes from the functional-traits analysis. The 9 fish species modeled in this study are shown as solid black circles. The remaining 127 native fishes of West Virginia (Ohio River Basin) are shown as gray circles. Functional traits that are strongly correlated with each axis are shown along their respective axes, with the direction of the correlation indicated by arrows. Light gray shaded regions indicate sections of the overall trait space that are not well represented by the 9 modeled species. The light gray shaded regions show that all but the largest species were included in our models and that lentic-type species are not well represented in our models. All other regions of the overall trait space are well represented.

River network, physical habitat, and climate data

We used the 1:100,000 scale National Hydrography Dataset Plus, Version 2 (NHDplus V2; McKay et al. 2012) digital stream network, clipped to the Ohio River Basin, as a common physical template for all fish occurrence records, environmental covariates (i.e., predictor variables), and SDMs. In the NHDplus V2, every digital stream segment has a unique "COMID" identifier that we used to cross-reference all fish occurrence and covariate data to their respective locations within the Ohio River Basin. We obtained physical habitat covariates from the NHDplus V2 attribute tables and the Stream-Catchment dataset (StreamCat; Hill et al. 2016). We selected these physical habitat covariates to represent 4 broad classes of potential effects on fish habitat: topographic, geologic, hydrologic, or urban.

We downloaded historical (1960–1990) and midcentury (2041–2060) climate data from WorldClim, Version 1.4 (Hijmans et al. 2005), as 30 arc-second–resolution grids. We captured midcentury data for 2 representative concentration pathway scenarios (RCPs): RCP 4.5 served as a mid-range emissions scenario (Thomson et al. 2011) and RCP 8.5 served as a high-range emissions scenario (Riahi et al. 2011). For both RCPs, we downloaded midcentury projections for 6 general circulation models: BCC-CSM1-1 (Wu et al. 2014), CCSM4 (Gent et al. 2011), GFDL-CM3 (Donner et al. 2011), GISS-E2-R (Schmidt et al. 2014), HadGEM2-CC (Martin et al. 2011), and MRI-CGCM3 (Yukimoto et al. 2012). We re-projected all climate grids to a common 1-km resolution grid spanning the entire Ohio River Basin. We calculated ensemble mean averages for both RCP 4.5 and RCP 8.5 for monthly air temperature and monthly precipitation in each 1-km grid cell. We performed all grid calculations in ESRI ArcMap 10.5 software (Environmental Systems Research Institute, Redlands, CA). We then appended gridded air temperature and precipitation values to the NHDplus V2 stream network by superimposing the climate grids directly onto the digital stream network, using System for Automated Geoscientific Analyses Version 2.1.4 software (Institute of Geography, Physical Geography Section, Hamburg University, Hamburg, DE). From these air temperature and precipitation data, we calculated mean annual streamflow for every digital stream segment in the Ohio River Basin using the Ohio River Basin-specific linear regression model of Vogel et al. (1999). We then calculated mean monthly stream temperatures using the logistic regression model of Segura et al. (2015).

Finally, we generated a Pearson correlation (r) matrix for all of the NHDplus V2, StreamCat, and derived climate variables (streamflow and stream temperatures) and used it to screen highly correlated covariates ($|r| \geq 0.70$) from the models. We selected a subset of 30 covariates that were potentially relevant to freshwater fishes from the remaining variables and transformed them, as necessary, for normality (see Table 1 for the complete covariate list with definitions, units of measure, and transformations).

Species distribution models

We used MaxEnt to build the SDMs because we were working solely with presence-only data (vs. presence–absence data; see Elith et al. 2006), and despite the

Table 1. List of the final 30 covariates that were considered in each of the Maximum Entropy species distribution models. Each covariate was calculated or interpolated at 1 of 2 spatial extents: an average value within the local catchment, or a discrete stream segment. For each covariate, units of measurement, data transformations (if applicable), and data sources are listed. [Table continued on following page.]

Covariate	Description	Spatial extent	Units	Transformation	Source
Area	Surface area of catchment	Catchment	km^2	ln(x + 1)	StreamCat
AvWetnessIndex	Mean wetness (composite topographic index) within catchment	Catchment	na	na	StreamCat
BarrenLand	Percent of catchment classified as barren land cover	Catchment	%	na	StreamCat
BFI	Base flow index as fraction of total flow due to base flow	Catchment	%	na	StreamCat
SiO_2	Percent lithological silicon dioxide content in near-surface geology within catchment	Catchment	%	na	StreamCat
CoalMines	Density of coal mines within catchment	Catchment	$Number/km^2$	ln(x + 1)	StreamCat
CropLand	Percent of local catchment classified as row crop land cover	Catchment	%	na	StreamCat
Elevation	Mean elevation within catchment	Catchment	m	na	StreamCat
Fe_2O_3	Percent lithological ferric oxide content in near-surface geology within catchment	Catchment	%	na	StreamCat
ForestLoss	Percent tree canopy cover loss throughout catchment and within 100-m buffer of stream channel	Catchment	%	ln(x + 1)	StreamCat
JanuaryPrecip	Mean January precipitation (1960-1990)	Stream	mm	na	WorldClim
JanuaryStreamTemp	Mean January stream temperature (1960–1990)	Stream	°C	na	Original calculation
JulyStreamTemp	Mean July stream temperature (1960–1990)	Stream	°C	na	Original calculation
JunePrecip	Mean June precipitation (1960–1990)	Stream	mm	na	WorldClim

Table 1, continued.

Covariate	Description	Spatial extent	Units	Transformation	Source
Mines	Density of mines and mineral plants within catchment	Catchment	Number/km^2	ln(x + 1)	StreamCat
NABD	Density of dams within catchment	Catchment	Number/km^2	ln(x + 1)	StreamCat
Nitrogen	Percent lithological nitrogen content in near-surface geology within catchment	Catchment	%	na	StreamCat
NPDES	Density of National Pollutant Discharge Elimination System sites within catchment	Catchment	Number/km^2	ln(x + 1)	StreamCat
OpenWater	Percent of catchment classified as open water	Catchment	%	na	StreamCat
OrganicMatter	Percent organic matter within catchment	Catchment	%	ln(x + 1)	StreamCat
RoadCrossings	Density of road-stream crossings within catchment	Catchment	Number/km^2	ln(x + 1)	StreamCat
Roads	Length of roads within catchment per unit surface area of catchment	Catchment	km/km^2	na	StreamCat
Runoff	Estimated runoff with catchment (1971–2000)	Catchment	mm	na	StreamCat
Sand	Percent sand in near-surface geology within catchment	Catchment	%	na	StreamCat
Slope	Slope of stream channel	Stream	m/m	ln	NHDplus v2
StreamOrder	Strahler stream order	Stream	na	na	NHDplus v2
Streamflow	Mean annual streamflow	Stream	m^3/s	ln(x + 1)	Original calculation
Superfund	Density of Superfund sites within catchment	Catchment	Number/km^2	ln(x + 1)	StreamCat
TRI	Density of Toxic Release Inventory sites within catchment	Catchment	Number/km^2	ln(x + 1)	StreamCat
WaterTableDepth	Mean water table depth within catchment	Catchment	cm	na	StreamCat

recent recognition that MaxEnt is only one of several methods to build point-process models (Renner et al. 2015), it remains among the most flexible and accessible software tools for doing so. Briefly, our modeling process was as follows. We used historical species occurrence and environmental covariate data to build a MaxEnt model for each of the 9 selected fishes. We created a background sample for each species by randomly selecting 20% of the complete landscape (i.e., 20% of all NHDplus V2 stream segments within the Ohio River Basin). To ease interpretation of individual covariate effects, we constrained the MaxEnt models to simple hinge and quadratic features (see Elith et al. 2011). We ran MaxEnt with a maximum of 10,000 background points, 500 iterations, and a convergence threshold of 0.00001.

For model development, we used prior knowledge of species' autecology and standard MaxEnt diagnostics to evaluate the 30 potential covariates and then selected a subset of covariates ($n \leq 9$; Moreno-Amat et al. 2015) that were the most effective predictors of a given species' occurrence (Fourcade et al. 2017, Petitpierre et al. 2016). Covariate evaluation was an iterative process that included standard MaxEnt percent contribution and permutation importance summary tables for individual covariates as well as covariate jackknife plots (Phillips 2017).

We used MaxEnt regularized training gain as an index of model fit. Regularized training gain is a measure of the distance between a multivariate distribution of covariates at randomly selected background sites (i.e., a random sample of the entire landscape that a species could potentially inhabit) and a corresponding distribution of covariates at sites of known species occurrences (Elith et al. 2011). Hence, a large training gain indicates an affinity for a narrow range of environmental conditions, relative to the broader landscape, while a small training gain suggests a lack of specialized habitat requirements (i.e., the distribution of covariates at occurrence sites mirrors the background distribution; Merow et al. 2013). We also used the exponential transformation of the MaxEnt regularized training gain for each SDM to aid in model evaluation. The exponential of the regularized training gain is the ratio of habitat suitability between sites of known occurrence and randomly selected background sites (Phillips 2017). Exponential values much larger than 1 are indicative of species with specialized habitat requirements; because these specialist species occupy a narrow range of habitats relative to the complete range of available habitats, SDMs can more efficiently discriminate between suitable and unsuitable habitat.

Notably, we did not use the replication features of MaxEnt (cross-validation, bootstrapping, or single-split subsampling; see Phillips 2017) to assess model generality. Our goal was only to model potential habitat suitability throughout the study landscape, not to predict the probability of presence at any given locality. Thus, we did not seek to estimate omission and commission error rates. Our study was designed to characterize a potential threat to freshwater fishes within a unique and highly context-specific scenario: upstream movement towards MTR sites in West Virginia. Transferability to other regions, where environmental conditions and MTR activity are almost certain to be different, was not an objective in our model-building exercises.

Once we had specified a final MaxEnt model for each fish species in the final subset, we projected habitat suitability to a midcentury time horizon (2041–2060) under the RCP 4.5 and RCP 8.5 climate change scenarios. We obtained the projections by substituting future values of the climate-driven covariates (streamflow, stream temperature, and precipitation) for the historical values used to build and parameterize each model. Then, by comparing aggregate distributions of MaxEnt raw output values among historical and future landscapes, we were able to estimate potential shifts in habitat suitability for each fish species.

Finally, we used a spatial querying process to identify stream segments that are likely to be impacted by MTR operations in the state of West Virginia. We began with a digital map of all active MTR permit boundaries from the West Virginia Department of Environmental Protection (http://tagis.dep.wv.gov/home/Downloads; downloaded on 24 October 2017). We built a 10-km–radius buffer around each of the MTR sites in ArcMap. The 10-km buffer provided an estimate of the potential spatial footprint of MTR effects on local aquatic ecosystems; in several instances, significant effects of MTR on aquatic biota have been documented at downstream distances >10 km (e.g., Bernhardt et al. 2012, Lindberg et al. 2011, Pond et al. 2008). By using the MTR buffer to query potentially impacted stream reaches from the complete river network, we were able to test the hypothesis that climate change is likely to increase exposure of West Virginian fishes to MTR.

We used the nonparametric one-sided Mann–Whitney *U* test to make comparisons between historical and future SDM projections (Woods and McGarvey 2018). This test compared the distribution of ranks between 2 unpaired datasets. The datasets were combined and each value was ranked from smallest to largest. We calculated the average ranks of the members of each group from this rank distribution; a large difference between the groups' mean ranks suggested the distributions were distinct. Future changes in habitat suitability were also expressed as percentages, relative to historical suitability, according to the formula: % change = (future median raw score - historical median raw score) ÷ historical median raw score × 100.

Results

Species selection

Following functional trait analyses, we selected a representative subset of 9 non-game fish species from the families Catostomidae, Cottidae, Cyprinidae, and Percidae (Table 2). These 4 families constitute the majority of native fish diversity in West Virginia (Stauffer et al. 1995), and an abundance of occurrence records was available for species in each family (Frimpong et al. 2016). Within families, we selected species in proportion to the overall richness of the respective family. For instance, we selected 4 from Cyprinidae, the most diverse family, but only 2 species from the less diverse Catostomidae. In general, the 9 selected species spanned the overall extent of the 2-dimensional trait-space represented by the native West Virginian fishes. We excluded from the representative subset only the largest fishes that reside in large, mainstem tributaries of the Ohio River (e.g., *Aplodinotus grunniens*

Rafinesque [Freshwater Drum]) or that prefer slow-flowing, lentic habitats in deep rivers and pools (e.g., *Notropis wickliffi* Trautman [Channel Shiner]) (Fig. 2).

MaxEnt models

Regularized training gain varied from 0.510 to 1.613 among the final SDMs. Though variable, the final covariate lists included in each of the models exhibited

Table 2. Summary information on the fit and structure of the Maximum Entropy (MaxEnt) species distribution models. For each species, the number of occurrence records (*n*) used to build the model and the MaxEnt regularized training gain (rtg) are shown with the exponential of the rtg in parentheses. MaxEnt % contribution and permutation importance diagnostics are also shown for each covariate that was retained in a species' final model. [Table continued on following page.]

Species	Covariate	% contribution	Permutation importance
Catostomidae			
Catostomus commersonii (Lacépède) (White Sucker)			
n = 2478	Catchment area	41.8	55.7
rtg = 0.614 (1.848)	Mean annual streamflow	24.4	11.8
	Mean June precipitation	11.7	11.1
	Catchment runoff	7.6	6.8
	Catchment road crossings	4.4	0.5
	Catchment BFI	4.2	2.3
	Catchment elevation	4.1	8.5
	Stream order	1.7	3.4
Hypentelium nigricans (Lesueur) (Northern Hogsucker)			
n = 2716	Catchment area	47.7	52.5
rtg = 0.565 (1.759)	Mean annual streamflow	31.6	27.6
	Catchment elevation	9.6	11.1
	Mean June precipitation	3.1	3.3
	Catchment road crossings	2.9	1.2
	Catchment BFI	2.7	2.1
	Catchment water table depth	2.3	2.3
Cottidae			
Cottus bairdii Girard (Mottled Sculpin)			
n = 893	Catchment BFI	18.0	6.7
rtg = 1.166 (3.209)	Catchment area	17.0	28.1
	Catchment elevation	16.7	25.3
	Catchment runoff	13.6	20.9
	Mean annual streamflow	13.5	10.3
	Catchment sand	9.0	4.7
	Catchment road crossings	6.5	0.6
	Mean June precipitation	5.7	3.3
Cyprinidae			
Campostoma anomalum (Rafinesque) (Central Stoneroller)			
n = 3156	Catchment area	42.1	46.6
rtg = 0.540 (1.716)	Mean annual streamflow	34.7	31.7
	Mean June precipitation	5.5	8.3
	Catchment elevation	5.2	7.1
	Catchment runoff	4.8	3.0
	Catchment road crossings	3.8	0.6
	Catchment BFI	2.3	1.1
	Catchment Fe2O3	1.4	1.5

some clear commonalities. Catchment area (percent contribution = 41.8–48.9%) and mean annual streamflow (percent contribution = 22.2–42.4%) were the 2 most important predictors of suitability in 6 of 9 models, and both variables were

Table 2, continued.

Species	Covariate	% contribution	Permutation importance
Notropis buccatus (Cope) (Silverjaw Minnow)			
n = 1892	Catchment runoff	28.4	7.1
rtg = 0.869 (2.385)	Mean annual streamflow	22.2	50.4
	Catchment area	21.4	5.9
	Catchment road crossings	8.1	1.2
	Catchment BFI	4.8	5.1
	Stream order	3.9	6.5
	Catchment open water	3.9	0.1
	Mean June precipitation	3.8	9.4
	Mean January precipitation	3.4	14.4
Luxilus chrysocephalus Rafinesque (Striped Shiner)			
n = 460	Mean annual streamflow	42.4	36.3
rtg = 1.613 (5.018)	Mean January precipitation	24.3	33.3
	Catchment area	8.6	6.4
	Catchment wetness index	7.9	2.8
	Catchment organic matter	5.9	6.1
	Catchment BFI	4.6	10.3
	Catchment runoff	4.4	2.4
	Catchment elevation	1.9	2.3
Semotilus atromaculatus (Mitchill) (Creek Chub)			
n = 3146	Catchment area	48.9	69.8
rtg = 0.510 (1.665)	Mean annual streamflow	31.8	13.8
	Catchment road crossings	7.0	1.1
	Mean June precipitation	5.0	5.3
	Catchment runoff	3.8	3.4
	Stream order	2.2	4.9
	Catchment elevation	1.3	1.7
Percidae			
Etheostoma blennioides Rafinesque (Greenside Darter)			
n = 2617	Catchment area	47.4	49.3
rtg = 0.597 (1.817)	Mean annual streamflow	30.8	27.1
	Catchment elevation	11.1	15.6
	Catchment open water	3.2	0.2
	Catchment runoff	3.1	4.5
	Catchment road crossings	2.6	0.3
	Mean January precipitation	1.8	2.9
Etheostoma caeruleum Storer (Rainbow Darter)			
n = 2365	Catchment area	42.8	43.2
rtg = 0.625 (1.868)	Mean annual streamflow	25.3	19.1
	Catchment elevation	16.9	22.3
	Mean January precipitation	5.4	7.3
	Catchment road crossings	4.9	0.2
	Catchment runoff	4.7	7.9

included in each of the final models (Table 2). Mean January or mean June precipitation was also included in all final models. Notably, stream temperature was not a strong predictor of suitability for any species and was thus excluded from all models. Complete MaxEnt results for each of the 9 modeled species, including sample sizes, model fit diagnostics, and indices of importance for individual covariates are shown in Table 2.

Interestingly, we found that the importance of some covariates tended to be preserved among species within a shared taxonomic affinity. For example, suitability was positively associated with catchment area and inversely related to streamflow for both *Etheostoma blennioides* (Greenside Darter) and *Etheostoma caeruleum* (Rainbow Darter). However, the shapes of the MaxEnt response curves for a given covariate were variable. For instance, habitat suitability was negatively associated with runoff of ~350–900 mm for the Rainbow Darter, but the runoff-response curve was bimodal with peaks at ~325 mm and ~900 mm for the Greenside Darter. We identified similar family-level responses to catchment area and streamflow among Catostomidae species and the Cyprinidae species, with the exception of *Luxilus chrysocephalus* Rafinesque (Striped Shiner), for which habitat suitability was positively associated with streamflow of ~0.1–3.4 m^3/s but declined at higher streamflow. Predicted suitability among the Cyprinids generally shared a negative association with June precipitation in the range of ~80–140 mm/y and with runoff of ~325–675 mm/y, with the Striped Shiner again standing out as the exception; June precipitation did not have a strong influence on Striped Shiner habitat suitability, but runoff of ~500–625 mm/y did. Individual covariate response curves are provided in the MaxEntReport html file for each species, available on Figshare (DOI:10.6084/m9.figshare.6106682).

Predicted habitat suitability

Under the RCP 4.5 climate scenario, significant increases (Mann–Whitney: $P < 0.001$) in habitat suitability were predicted within the MTR buffer for the 2 darters (*Etheostoma*), but none of the remaining species (Fig. 3). Under the RCP 8.5 scenario, however, habitat suitability was predicted to significantly increase within the MTR buffer for 8 of 9 species. Percent increases in median habitat suitability under the RCP 8.5 scenario varied from 46% to 418%, relative to the historical habitat suitability values, with a grand median increase of 125% (Fig. 3). Only *Notropis buccatus* (Silverjaw Minnow) was predicted to experience a decrease in habitat suitability within the MTR buffer. Maps of MaxEnt raw scores for the Striped Shiner within the MTR buffer under the historical, RCP 4.5, and RCP 8.5 scenarios are shown in Figure 4. Summary distributions of all MaxEnt habitat suitability predictions are illustrated in Figure 3.

Discussion

Climate-change effects: hydrology vs temperature

Using MaxEnt SDMs for 9 representative species, we tested the hypothesis that climate change is likely to drive directional, upslope shifts in habitat suitability for

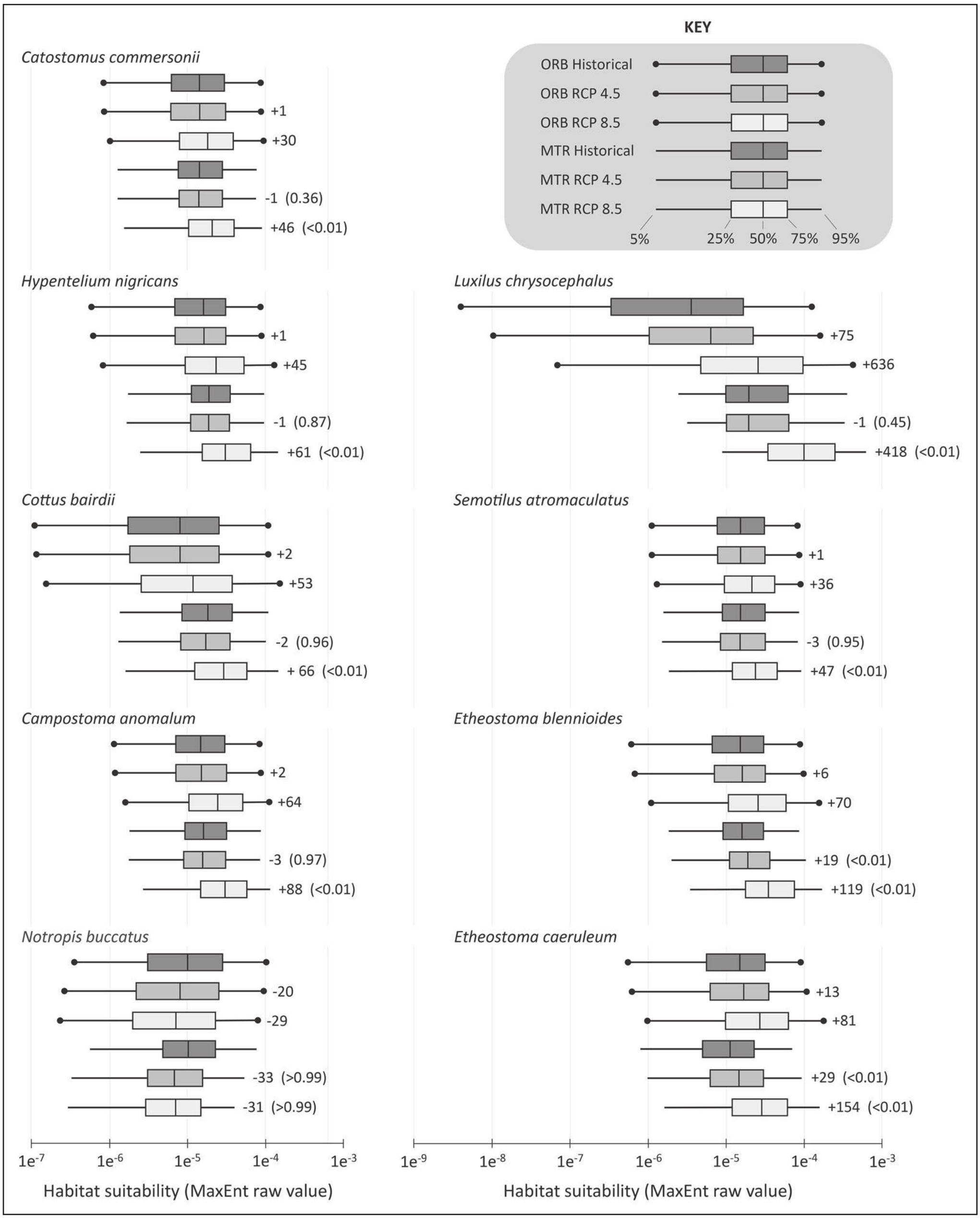

Figure 3. Boxplots of the distributions of MaxEnt raw scores. Box elements are standard percentiles (see key). For each species, the distributions of raw scores across the Ohio River Basin (ORB and within the mountaintop removal buffer (MTR) are shown for historical data as well as the RCP 4.5 and RCP 8.5 midcentury climate-change scenarios. Percent differences in median MaxEnt raw scores, comparing historical averages with future RCP 4.5 and RCP 8.5 averages, are shown for ORB and MTR data at right of each box. Mann-Whitney test *P*-values (paired sample tests using individual stream segments as replicates) comparing historical MaxEnt raw scores with future projections are also shown in parentheses for the RCP 4.5 and RCP 8.5 results within the MTR buffer.

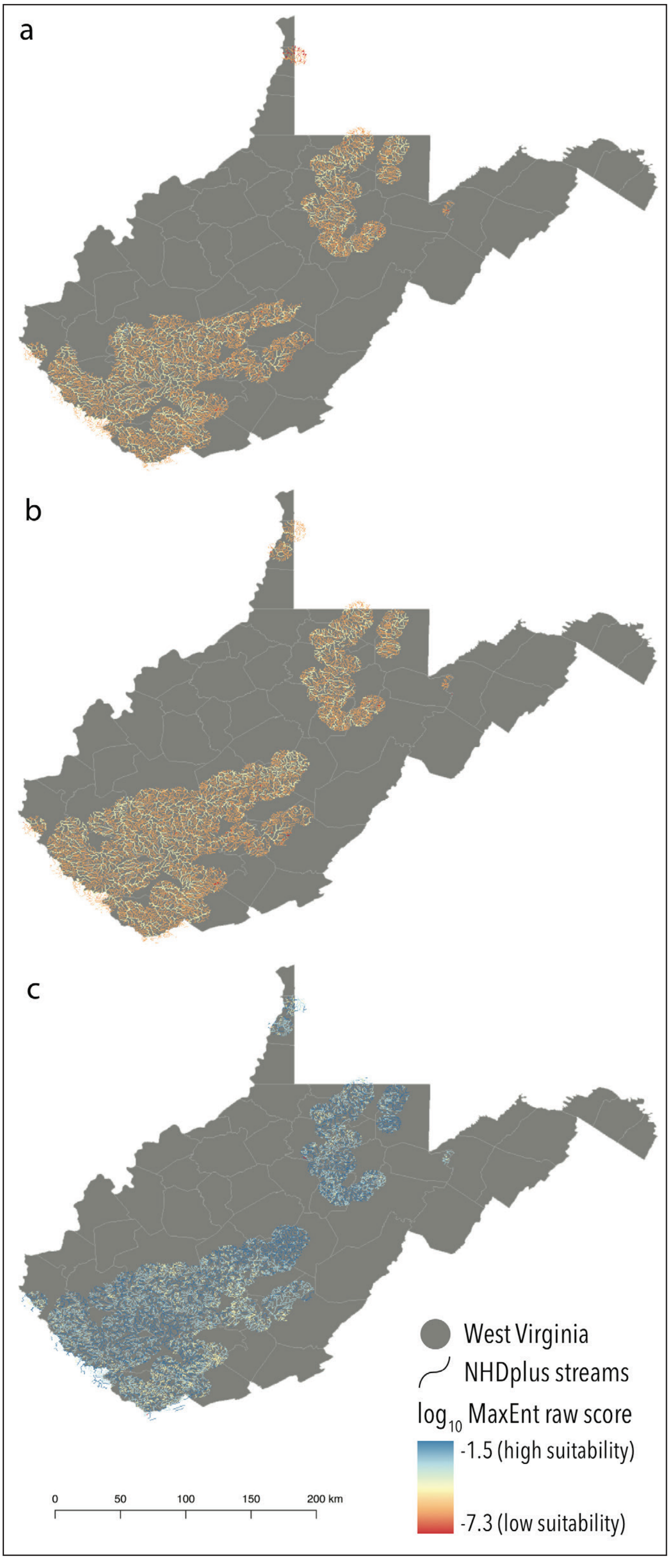

Figure 4. Maps of MaxEnt raw scores for the Striped Shiner within the MTR buffer under the (a) historical, (b) RCP 4.5, and (c) RCP. 8.5 scenarios. Maximum suitability scores are shown in blue and minimum suitability scores are shown in red.

West Virginian freshwater fishes, thereby placing the best habitats in close proximity to MTR operations. In many instances, our results supported this hypothesis, but the support was conditional, varying among species and climate-change scenarios. Furthermore, we were surprised by the factors that ultimately drove the shifts in habitat suitability. Ambient temperature is a fundamental regulator of niche space for ectotherms (Coulter et al. 2014, Deutsch et al. 2008); thus, we expected stream temperature to be a key predictor of fish habitat suitability. This was not the case, however, and stream temperature was not included in any of the final models (see Table 2).

The apparent lack of a strong temperature effect may indicate that the modeled species have relatively broad thermal tolerances. At historical occurrence sites, the widest ranges of winter and summer stream temperature values for a given species (i.e., stream temperature ranges among all sites of known presence) spanned 2.74 °C for *Semotilus atromaculatus* (Creek Chub) (min. = 0.38 °C, max. = 3.12 °C) and 6.24 °C for the Silverjaw Minnow (min. = 22.72 °C, max. = 28.96 °C), respectively. Conversely, the narrowest ranges of historical winter and summer stream temperatures for a given species spanned 2.62 °C for the Striped Shiner (min. = 0.40 °C, max. = 3.02 °C) and 5.53° C for *Cottus bairdii* (Mottled Sculpin) (min. = 23.36 ° C; max. = 28.89 °C), respectively. In all cases, species' historical winter and summer temperature ranges encompassed a large fraction of the historical temperature range across the entire Ohio River Basin; historical winter and summer stream temperatures spanned 2.76 °C (min. = 0.36 °C, max. = 3.12 °C) and 6.32 °C (min. = 22.69 °C, max. = 29.01 °C), respectively.

Together, these observations suggest that each of the 9 modeled fishes would be physiologically capable of occupying most or all of the streams in the Ohio River Basin, if mean winter or summer stream temperature were the sole determinant of habitat suitability. The fact that documented occurrences of each of the modeled species were limited to a subset of streams within the Ohio Basin suggests that factors other than stream temperature are fundamental in regulating fish species' presences. With specific reference to MaxEnt, the fact that historical sample temperatures exhibit so much overlap with the background temperatures indicates that mean winter and summer stream temperatures may not be useful for discriminating between suitable and unsuitable fish habitat.

Instead, species' responses to climate change were driven primarily by hydrology. In each model, hydrologic variables were among the best predictors of fish occurrence (Table 2). For example, mean annual streamflow was included in every model, and in 8 of 9 cases, it was the first or second most-influential covariate when ranked by MaxEnt percent contribution statistics (13.5–42.4%). Other covariates that represent hydrology or a dimension of the hydrologic cycle included summer and winter precipitation (one of which was included in every model), runoff (included in 8 of 9 models), and the baseflow index (included in 6 models). Importantly, these different hydrology covariates did not provide redundant information. When calculated across the entire Ohio River Basin, Pearson correlation coefficients among these covariates never exceeded the collinearity threshold of $|r| > 0.70$

and in several instances were much lower. For instance, correlations between mean annual streamflow and January precipitation and between streamflow and June precipitation were $r < 0.01$ and $r = -0.40$, respectively. Furthermore, January and June precipitation were not highly correlated ($r = 0.35$). Thus, we concluded that the various hydrologic covariates (streamflow, precipitation, runoff, baseflow index) represented different dimensions of the hydrologic cycle and were therefore appropriate for inclusion in the same models.

In retrospect, the strong effect of hydrology was not surprising, given that hydrology is widely regarded as a master variable in lotic ecosystems (Poff et al. 1997). Streamflow is a dynamic integration of many physical processes occurring across the landscape. Though it is clearly a function of precipitation, streamflow is also influenced by the geologic and antecedent factors that regulate surface runoff, soil water, and groundwater dynamics (Poff et al. 1997). In this way, streamflow becomes an efficient indicator of many different yet interrelated influences on aquatic habitat (McGarvey and Terra 2016). Effects of these hydrologic influences include direct, individual-level physiological and behavioral mechanisms (Mims and Olden 2011, Poff and Allan 1995, Poff et al. 1997) as well as emergent patterns in species' distributions and overall richness (McGarvey 2014, Power et al. 1995, Wenger et al. 2011). We therefore believe it is logical that streamflow, rather than stream temperature, proved to be a primary determinant of habitat suitability in the fish models.

It should be noted that our hydrologic variables did not account for potential effects of MTR on streamflow (Evans et al. 2015). Disruptive effects of MTR on local flow include large-scale deforestation and the resulting decreases in evapotranspiration and groundwater recharge, as well as increased surface runoff via soil compaction from heavy machinery operation (Griffith et al. 2012). These alterations may lead to elevated peak-flow conditions downstream from MTR sites (Nippgen et al. 2017, Wiley et al. 2001), but observed downstream effects have so far been variable across spatial and temporal scales (Evans et al. 2015, Ross et al. 2016, Zegre et al. 2014). Due to this variability, it is difficult to predict if or how climate-driven changes in hydrology may simultaneously be affected by MTR, but it is plausible that future hydrology in the immediate vicinity of MTR sites may deviate from our predicted conditions, with unknown effects on fish habitat suitability.

Differential responses to climate change

Of the 9 modeled species, the 2 *Etheostoma* spp. may be the most likely to shift their ranges upstream in response to climate change. The Greenside Darter and Rainbow Darter were the only species predicted to experience significant increases in habitat suitability within the MTR buffer under both climate change scenarios (Fig. 3). For all other species, significant increases in habitat suitability were limited to the RCP 8.5 scenario. This responsiveness to both scenarios was driven by the strong influence of January precipitation on darter habitat suitability. Increasing levels of January precipitation within the MTR buffer were evident among the historical (mean = 83.8 mm; sd = 6.3 mm), RCP 4.5 (mean = 92.9; sd = 7.3), and RCP 8.5 (mean = 99.2; sd = 8.3) datasets. Predicted suitability for both *Etheostoma* spp. was, in turn, positively associated with January precipitation, particularly with totals of ~40–100 mm/month. Should January precipitation exceed 100 mm/month, however, habitat suitability is likely to decrease (see MaxEnt response-curve plots in the MaxEntReport html file for each species, available on Figshare; DOI:10.6084/m9.figshare.6106682.) We therefore suggest that the projected moderate to large increases in winter precipitation are likely to make habitat in high-elevation streams in West Virginia more suitable for Greenside Darter and Rainbow Darter.

Currently, we do not know what specific mechanism might link winter precipitation to *Etheostoma* habitat. Both darters in this study lack air bladders and reside in benthic, riffle habitats, often sheltering from fast currents behind large rocks or woody debris (Fahy 1954, Harding et al. 1998). This tendency to avoid suspension in fast water is consistent with our observation that *Etheostoma* habitat suitability decreased with increasing mean annual streamflow (each species' response curve for streamflow is available in the respective MaxEntReport, available, as above, on Figshare; DOI:10.6084/m9.figshare.6106682). This result seems counterintuitive, in light of the seeming preference for higher winter precipitation, which should increase mean annual streamflow. One parsimonious explanation is that pulses in winter flow may prevent coarse riffle substrates from becoming embedded with fine sediments, thereby maintaining the critical physical habitats that *Etheostoma* darters utilize year-round. This dynamic was documented for a Greenside Darter population in the Grand River, ON, Canada (Bunt et al. 1998) and, if it is similarly applicable in streams in West Virginia, it is cause for heightened concern because increased fines and sedimentation are common byproducts of MTR (Griffith et al. 2012, Nelson et al. 1991).

January precipitation and mean annual streamflow were also key predictors of habitat suitability for the Striped Shiner. However, the effect of streamflow differed from the effect on habitat of *Etheostoma* spp. Striped Shiner habitat suitability increased rapidly with increasing streamflow (see MaxEntReport on Figshare), rather than decreasing from a low modal streamflow value as it did for *Etheostoma* spp. This finding accounts for the dramatic increase in Striped Shiner habitat suitability under RCP 8.5 (Fig. 3); a large increase in mean annual streamflow is expected within the MTR buffer under RCP 8.5 (mean = 0.18 m^3/s; sd = 0.51 m^3/s; streamflow values are transformed (ln[x+1]), relative to historical streamflow (mean = 0.06; sd = 0.22). However, a comparable increase in streamflow is not expected under RCP 4.5 (mean = 0.06; sd = 0.24). Thus, a significant increase in Striped Shiner habitat suitability was not predicted for RCP 4.5 (Fig. 3).

Predicted increases in habitat suitability for 2 of the remaining species of Cyprinidae, the Creek Chub and *Campostoma anomalum* (Central Stoneroller), as well as all species of Catostomidae and Cottidae, were also driven mean annual streamflow. For each species, maximum habitat suitability occurred at a relatively low streamflow value, then decreased to a stable, asymptotic level with increasing streamflow (see streamflow response curves in MaxEntReports on Figshare;

DOI:10.6084/m9.figshare.6106682).For example, habitat suitability for the Creek Chub peaked at a mean annual streamflow value of ~0.02 (in natural log transformed units) then rapidly decreased at higher streamflows. In these cases, the most suitable streamflow values were similar to the average streamflow values predicted within the MTR buffer for RCP 8.5 (median streamflow = 0.012 in natural log units), but not for RCP 4.5 (median streamflow = 0.002). Thus, significant increases in habitat suitability within the MTR buffer were limited to the RCP 8.5 scenario.

Decreasing habitat suitability within the MTR buffer was predicted only for the Silverjaw Minnow (Fig. 3) and was due to the strong, negative associations that mean annual streamflow and precipitation had with habitat suitability. For each of these covariates, suitability peaked at a low value then rapidly decreased (see response curves on Figshare). These modeling observations are consistent with field studies that showed the Silverjaw Minnow is often abundant in small streams but highly sensitive to periods of low-flow drought and to high-flow events (Toth et al. 1982, Wallace 1972). In theory, the decreasing suitability of stream habitat within the MTR buffer might serve to protect the Silverjaw Minnow; this species is unlikely to be impacted by MTR if it does not inhabit streams near MTR operations. Unfortunately, the Silverjaw Minnow will experience no net benefit if the availability of small streams that it has historically occupied is greatly diminished by climate change.

Are the model predictions cause for concern?

Our results suggest that, in a warming climate, habitat suitability for 8 of the 9 modeled species is likely to increase in high-elevation streams near MTR operations. However, we cannot prove that any of our predicted changes in habitat suitability will come to pass, or that the study species will in fact migrate to streams within the MTR buffer. We therefore conclude with some general thoughts on the relevance of our modeling process and findings.

First, we emphasize that the RCP 4.5 and 8.5 climate change scenarios, though heuristic in nature, are broadly recognized by the scientific community as valid and entirely plausible. Indeed, Smith et al. (2011) have shown that global warming of 2 °C beyond pre-industrial levels may be achieved as early as 2030 and that 4 °C warming may occur as soon as 2060. Similarly, Betts et al. (2011) estimate global mean temperature will increase by 4 °C above pre-industrial levels between 2060 and 2070. Others propose global mean temperature is highly likely to exceed the benchmark of 2 °C by 2030, citing a likely temperature increase of from 2 °C to 4.9 °C by 2100 (Raftery et al. 2016). Collectively, these reports show, despite uncertainty, that the range of outcomes bracketed by the RCP 4.5 and RCP 8.5 climate scenarios are plausible and could be reached by midcentury.

Second, there are relatively few migration barriers in the rivers and streams of West Virginia that would categorially prevent fishes from migrating to higher elevations near MTR sites. Numerous lock-and-dam structures that may constrain movement and reduce population connectivity exist along the mainstem Ohio, Kanawha, and Monongahela rivers in West Virginia, but these structures are at least semi-permeable to fish movement (Argentina et al. 2018). In general, the number of large, impassible dams on westward-flowing Ohio River tributaries is modest in comparison to other eastern US states (USACE 2016). Using a GIS, we performed a manual search for large, impassible dams that would prevent upstream fish movement and identified 10: Hawks Nest (inclusive of all upstream dams on the mainstem New River and Kanawha Falls, ~5 km downstream of Hawks Nest Dam), Summersville, Sutton, Taylor Fork, Shannonpin Mine, Cheat Lake, Tygart, R.D. Bailey, Upper Mud River No. 2A, and East Lynn. The total length of stream channel that was upstream of any of these barriers and within the MTR buffer was 1445 km, or ~9% of the 15,732 km of total stream channel within the buffer.

Less-conspicuous barriers could also constrain future fish movement. For instance, road crossings and culverts often impede fish movement (Januchowski-Hartley et al. 2013, Warren and Pardew 1998). This barrier is a point of concern because the density of road crossings was a good predictor of fish occurrence, and therefore selected as a final predictor variable, for 8 of the 9 modeled species (Table 2). Currently, we do not have comprehensive data that could be used to incorporate road crossings into our analyses in a spatially explicit manner, but we do note that most of the fishes in this study have broad ranges that historically include some mid- to high-elevation streams. Thus, it is likely that even in a landscape that is highly fragmented by road crossings, some potential colonists are already present near the MTR buffer sites and therefore capable of moving to them in a changing climate.

Finally, we submit that our specific results should be broadly representative of the native stream ichthyofauna of West Virginia. Functional-trait analysis indicated that the selected model species covered much of the functional trait space encompassed by all Ohio River Basin fishes of West Virginia (Fig. 2). Furthermore, the 4 families represented by our selected subset—Catostomidae, Cottidae, Cyprinidae, and Percidae—include 114 non-game fish species and represent 65% of all native fishes in West Virginia (Stauffer et al. 1995). As noted above, the model-predicted shifts in high-elevation habitat suitability were generally positive (i.e., increasing suitability) for 8 of 9 species. Thus, we believe it is logical to predict that habitat suitability for many of the remaining fishes will respond in a similar manner.

Although we did not model MTR effects on fishes per se, we posit that the predicted tendency for habitat suitability to increase near MTR sites is, of itself, legitimate cause for concern. The most acute, negative effect of MTR on freshwater fishes will be direct habitat loss as MTR overburden is dumped as valley-fill, effectively eliminating headwater streams. Further downstream, chemical contaminants will accumulate through leaching and as coal is washed to lower its sulfur content. Toxicants from MTR are known to cause infertility (Palmer et al. 2010), teratogenic deformities (Palmer et al. 2010), and death among individual fishes (Ferreri et al. 2004), as well as population- and assemblage-level declines in fish abundance and diversity (Ferreri et al. 2004, Hitt and Chambers 2014). In southern

West Virginia, more than 750 km of high-elevation streams have already been buried by MTR waste, and chronic effects of MTR are now impacting 2800–4300 km of additional stream habitat (Bernhardt et al. 2012). Thus, we conclude that the combined effects of climate change and MTR are likely to pose very real and significant threats to many of West Virginia's native freshwater fishes by midcentury.

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