



Random Frogs: using future climate and land-use scenarios to predict amphibian distribution change in the Upper Missouri River Basin

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Abstract

Context Climate change and anthropogenic stressors have contributed to rapid declines in biodiversity worldwide, particularly for amphibians. Amphibians play important ecological roles, yet little is known about how distribution hotspots may change or how the environmental factors influence distribution patterns in the North American Great Plains.

Objectives Ecological niche models improve understanding of biotic and abiotic factors associated with species' distributions and can highlight potential threats to species conservation. Here, we identify important predictors of amphibian distributions and

predict how land use and climate change may alter amphibian distributions in the Upper Missouri River Basin.

Methods We used publicly available occurrence data, 16 environmental and climatic predictors, and the machine-learning algorithm, Random Forests, to create spatially explicit distribution models for eight amphibian species. Models were scored to baseline conditions (2005) and two future climate-change/land-use scenarios to predict changes in amphibian distributions for 2060.

Results Models were highly accurate and revealed more pronounced distribution changes under the intensive RCP8.5/CONUS A2 scenario compared to the moderate RCP6.0/CONUS B2 scenario. Both scenarios predicted gains for most eastern species (i.e., Blanchard's cricket frogs, Plains leopard frogs, Woodhouse's toads, and Great Plains toads) and declines for all western montane species. Overall, distribution changes were most influenced by climatic and geographic predictors, (e.g., mean temperature in the warmest quarter, precipitation, and elevation), and geography, versus anthropogenic land-use variables.

Conclusions Changes in occurrence area varied by species and geography, however, high-elevation western species were more negatively impacted. Our distribution models provide a framework for conservation efforts to aid the persistence of amphibian species across a warming, agriculturally dominated landscape.

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Introduction

Amphibians are the most imperiled taxonomic class of vertebrates worldwide (Hoffmann et al. 2010) resulting from the synergistic effects of habitat conversion, wetland contamination, invasive species, disease, and climate change (Sodhi et al. 2008; Johnson et al. 2011; Adams et al. 2013; Bradley et al. 2019). Although numerous taxonomic groups have recently experienced human-caused biodiversity loss, amphibian population declines have been particularly severe (Stuart et al. 2004; González-del-Pliego et al. 2019). In North America, the highest amphibian biodiversity occurs in the southeastern United States and in the temperate rainforests along the west coast (Dodd 1997; Battaglin et al. 2005; Graham et al. 2010; McKerrow et al. 2018). These areas are subject to the same threats causing global declines in amphibian diversity and abundance, especially as deforestation, wetland conversion, and pollution continue to shrink available habitat (Mushet et al. 2014; Todd et al. 2014; Sievers et al. 2017).

The effects of climate change on amphibians are threatening the survival of numerous species by altering phenological cues for spring emergence (Buss et al. 2021) and shifting available temperature ranges surrounding biological processes (Fontaine et al. 2018), forcing species to rapidly adapt or migrate to remain within thermal optima (Enriquez-Urzelai et al. 2019). For example, amphibians have a bi-phasic (aquatic and terrestrial) lifestyle and many of their biological and reproductive processes rely on narrow environmental temperature and moisture ranges, and so amphibians are especially sensitive among vertebrates to climate induced stressors and abrupt changes in land use (Zellmer et al. 2020). Additionally, many species have limited capacities for long-range movements and are unable to escape current microclimates as they become increasingly uninhabitable. As distributions shift and community compositions change, species will likely encounter new stressors in the form of competition from native and non-native species, predation, and disease. Stressors stemming from novel

community arrangements will likely result in altered species interactions and trophic changes (Williams and Jackson 2007; Brambilla et al. 2020).

In addition to climate change stressors, land use changes, particularly in agricultural regions, are also altering the amount and quality of available habitat. One such land use change involves the conversion of land to grow biofuel crops. Bioenergy with Carbon Capture and Storage (BECCS) has been proposed as a means of mitigating climate change by cultivating bioenergy crops (e.g., switchgrass [*Panicum virgatum*], canola [*Brassica napus*], soybeans [*Glycine max*]) that sequester atmospheric carbon into plant tissues, which can then be harvested and converted into heat, electricity, liquid or gas fuels (“bioenergy”; Stoy et al. 2018). Carbon emissions produced during bioenergy conversion are captured and deposited in geological formations (“carbon capture and storage”), which could theoretically result in negative emissions and a reduction in atmospheric carbon. However, implementing BECCS would require dramatic land use changes that may further degrade amphibian habitat, water quantity and quality (Hu et al. 2020), while also contributing to biodiversity losses (Mushet et al. 2014; Baltensperger et al. 2020). Here we examine the influence that land use changes associated with biofuel cultivation may have on amphibian distributions in the agriculturally dominant Upper Missouri River Basin (UMRB).

In the UMRB, several amphibian species have already experienced population declines, including Blanchard’s cricket frogs (*Acris blanchardi*), Western toads (*Anaxyrus boreas*), and Columbia spotted frogs (*Rana luteiventris*; Burdick and Swanson 2009, Pilliod et al. 2015, Slough and deBruyn 2018). Many of the surviving wetlands in the UMRB are located within agricultural landscapes and are at high risk of being converted to cropland, even during exceptionally wet years (Johnston and McIntyre 2019). Agricultural production will likely need to increase by approximately 60% over the next four decades and will result in the drainage of prairie pothole wetlands with significant habitat loss, decreased habitat connectivity, and population declines for many midwestern amphibian species unless substantial conservation protections are enacted (Wright 2010).

Amphibian richness in the UMRB is low due to the arid conditions that limit the number of species able to exist under these conditions (Lannoo 2005).

In response to elevated atmospheric carbon concentrations and resultant climate effects, amphibians in the U.S. may be shifting their distributions as they track temperature and precipitation conditions suitable to their sensitive physiological and phenological needs. Yet how and to what degree climate and land use change will affect amphibian distributions in the central U.S. remains unquantified. To address these gaps, we developed predictive landscape models to describe projected distribution and assemblage changes in the UMRB under a range of future climate and land use scenarios.

As amphibian populations dwindle, it is paramount to identify how drivers of these declines are likely to change species distributions. Species distribution models (SDM), also known as ecological niche models (ENM), are commonly used to identify important biotic and abiotic factors that predict baseline species distributions as well as future distributions based on climate and land use change projections to identify spatially explicit threats to species across broad landscapes (Oberhauser and Peterson 2003; Elith et al. 2006; Baltensperger and Huettmann 2015a, b; Kandel et al. 2015; Baltensperger et al. 2020). We used the machine-learning algorithm, Random Forests (RF),

which is adept at deciphering complex, non-linear, multi-variate relationships (Breiman 2001; Elith et al. 2006) to estimate baseline distributions of eight amphibian species across the UMRB using publicly available occurrence data attributed with 16 environmental and climatic predictors. We also projected future distribution changes using sets of ensemble climate predictions for 2060. Our models help to identify spatial effects of climate change and land use scenarios on amphibian distributions in a highly modified landscape over time. We use results to identify species and geographic areas at the highest risk of distribution losses in the UMRB.

Materials and methods

Study area

The UMRB is the largest watershed in North America and comprises approximately one-sixth of the conterminous United States, including parts of Montana, Wyoming, North Dakota, South Dakota, and north-central Nebraska (Fig. 1). Much of the UMRB is covered by grasslands and an abundance of shallow,

Fig. 1 Map of the Upper Missouri River Basin study area (grey outline) superimposed on the contiguous United States



isolated wetlands (known as prairie potholes), which provide habitat for a wide range of amphibians (Balas et al. 2012) as well as numerous ecosystem services including, carbon sequestration (Euliss et al. 2006), flood control, and the recharging of ground water aquifers that provide drinking water (Murkin 1998). This region is also known for its highly fertile soil and agricultural production. During the nineteenth and twentieth century grassland areas were extensively developed and more than 98% of wetlands were drained to make room for row crops and irrigation systems (Dahl 2000; Johnston 2013). The UMRB also overlaps with the Bakken Shale Formation, which is a hotspot for oil and gas extraction, and where increased development has contributed to the conversion of grassland and wetland habitat while further degrading water quality (Preston et al. 2019). We used the UMRB study area (746,787 km²) previously defined by Stoy et al. (2018), for which spatially contiguous land-use change scenarios were available. This area was also used in a broader effort (WAFERx project) to understand the effects of BECCS on the UMRB (Baltensperger et al. 2020; Amirkhiz et al. 2021).

Training data

We downloaded georeferenced occurrence records between 1902 and 2022 for Great Plains toads (*Anaxyrus cognatus*), Woodhouse's toads (*Anaxyrus woodhousii*), Blanchard's cricket frogs (*Acris blanchardi*), Plains leopard frogs (*Rana [Lithobates] blairi*), Western toads (*Anaxyrus boreas*), Rocky Mountain tailed frogs (*Ascaphus montanus*), Columbia spotted frogs (*Rana luteiventris*), and American toads (*Anaxyrus americanus*) from the Global Biodiversity Information Facility (GBIF; www.gbif.org; Derived dataset GBIF.org 2023). We supplemented these data with occurrence records provided by Burdick and Swanson (2009), the South Dakota Natural Heritage Program, Montana Natural Heritage Program, and HerpMapper (www.herpMapper.org) in 2019 (Online Resource 1 in Supplemental Material). To maximize model accuracy, we removed occurrence records with geocoding errors and locational uncertainty > 500 m from training datasets. Only records within the UMRB were included in models and we removed duplicates within 1 km (i.e., the same resolution as geospatial predictors).

Some species (i.e., Woodhouse's toads and Great Plains toads) had unevenly distributed presences due to unequal sampling intensity across the study area. This primarily occurred in datasets from the Montana Natural Heritage Program due to more frequent and rigorous sampling in the region. To account for spatial biases, we calculated the average distance between points in the datasets outside Montana and then thinned the Montana datasets by this value using the *Delete Identical* tool in ArcMap 10.5 (ESRI, Inc., Redlands, CA). For example, the average distance between presence points for Woodhouse's toads was 48,781 m, so we thinned the Montana dataset by 48,700 m and then merged both datasets to create a single set of presences for Woodhouse's toads.

As occurrences represented presence-only datasets, we generated sets of background 'pseudo-absences' in ArcMap 10.5 using the *Create Random Points* tool. Pseudo-absences are commonly used when 'true absence' data are not available and result in more accurate models compared to presence-only models (Elith et al. 2006; Barbet-Massin et al. 2012). Numbers of pseudo-absences were tailored for each target species, so that the densities of pseudo-absences equaled that of presences, using the following formulae and solving for X:

$$\frac{\text{\# of presence points}}{\text{minimum bounding geometry area}} = \frac{X}{\text{size of study area}}$$

$$\begin{aligned} \text{Example for } \textit{Acris blanchardi} &: \frac{139}{17,710.2} \\ &= \frac{X}{746,787} X = 5,861 \text{ pseudo absences} \end{aligned}$$

We used these formulae for all species, with the exception of Great Plains toads whose model contained twice as many pseudo-absences, to reduce background noise across its large range. We combined presence-only datasets and pseudo-absences to create training datasets, which we attributed with 16 spatial environmental predictors and then used to train ENM models. We attributed training datasets for each species with environmental predictor rasters using R (R Development Core Team 2017) in RStudio (RStudio Team 2020; Version 1.4.1103). Predictors were selected based on known or hypothesized effects on amphibian populations and ecology (Table 1; Funk et al. 2005; Green et al. 2013; Youngquist et al. 2017; Dare et al. 2020).

Table 1 Environmental predictors used in models, data type (continuous or categorical), and whether predictors change across time (static or dynamic). Continuous data had a 30-m resolution while categorical data had a 1-km resolution. We downloaded and used decadal climate ensemble data from 17 CMIP5 (Coupled Model Intercomparison Project Phase 5) model predictions for future climatic projections that reflect the moderate (RCP 6.0) and high (RCP 8.5) emissions sce-

narios for 2060 (Rehfeldt et al. 2006). All temperature values are in tenths of °C and all precipitation values are in mm. CONUS historical landcover (2005) was used for ‘baseline’ landcover data and was obtained from Sohl et al. (2018). All distance related predictors were calculated using the *Euclidean Distance* tool in ArcGIS 10.3. Derived predictor layers can be accessed at: <https://osf.io/8wu5e/>

Variable name	Data type	Temporal stability	Source
Aspect	Continuous	Static	Derived in ArcGIS from 30 m DEM; units are degrees (0–359)
Distance to Dams	Continuous	Static	Derived from the National Hydrography Dataset (NHD); 2018; units are meters to the nearest dam; https://www.usgs.gov/national-hydrography/access-national-hydrography-products
Distance to Lakes	Continuous	Static	Derived from the National Hydrography Dataset (NHD); 2018; units are meters to nearest lake; https://www.usgs.gov/national-hydrography/access-national-hydrography-products
Distance to Rivers	Continuous	Static	Derived from the National Hydrography Dataset (NHD); 2018; units are meters to nearest river; https://www.usgs.gov/national-hydrography/access-national-hydrography-products
Distance to Streams	Continuous	Static	Derived from the National Hydrography Dataset (NHD); 2018; units are meters to nearest stream; https://www.usgs.gov/national-hydrography/access-national-hydrography-products
Distance to Pollution Source	Continuous	Static	Derived from FRS Facilities Database; 2018; units are distance to nearest pollution point source in meters; https://www.epa.gov/frs/geospatial-data-download-service
Distance to Wetlands	Continuous	Static	Derived from U.S. Fish & Wildlife Service; National Wetlands Inventory; 2018; units are distance in meters to nearest wetland; https://www.fws.gov/program/national-wetlands-inventory/wetlands-data
Elevation (DEM)	Continuous	Static	The National Elevation Dataset (NED); 2007–2014; units are meters above sea level; https://apps.nationalmap.gov/downloader/
Geology	Categorical	Static	United States Geological Survey (USGS); Earth Resources Observation and Science (EROS) Center; 2016; units are types of bedrock; https://usgs.gov/centers/eros/data
Land Status	Categorical	Static	Conservation Biology Institute; Protected Areas Database of the US, PAD-US (CBI Edition); version 2.1 (2011); https://databasin.org/datasets/f10a00eff36945c9a1660fc6dc54812e/
Terrain Ruggedness	Continuous	Static	United States Geological Survey (USGS); The National Elevation Dataset (NED); derived from DEM; units are degrees
Slope	Continuous	Static	United States Geological Survey (USGS); The National Elevation Dataset (NED); derived from DEM; units are degrees
Historical CONUS FORE-SCE Landcover (1992–2005)	Continuous	Dynamic	United States Geological Survey (USGS) (Sohl et al. 2018); https://www.sciencebase.gov/catalog/item/5b96c2f9e4b0702d0e826f6d

Table 1 (continued)

Variable name	Data type	Temporal stability	Source
CONUS FORE-SCE A2 Landcover (2006–2100)	Continuous	Dynamic	United States Geological Survey (USGS) (Sohl et al. 2018); https://www.sciencebase.gov/catalog/item/5b96c2f9e4b0702d0e826f6d
CONUS FORE-SCE B2 Landcover (2006–2100)	Continuous	Dynamic	United States Geological Survey (USGS) (Sohl et al. 2018); https://www.sciencebase.gov/catalog/item/5b96c2f9e4b0702d0e826f6d
Winter precipitation (1961–1990)	Continuous	Dynamic	https://charcoal2.cnre.vt.edu/climate/current/ ; units are in millimeters
Winter precipitation (2060) – RCP6.0	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in millimeters
Winter precipitation (2060) – RCP8.5	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in millimeters
Spring precipitation (1961–1990)	Continuous	Dynamic	https://charcoal2.cnre.vt.edu/climate/current/ ; units are in millimeters
Spring precipitation (2060) – RCP6.0	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in millimeters
Spring precipitation (2060) – RCP8.5	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in millimeters
Summer precipitation (1961–1990)	Continuous	Dynamic	https://charcoal2.cnre.vt.edu/climate/current/ ; units are in millimeters
Summer precipitation (2060) – RCP6.0	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in millimeters
Summer precipitation (2060) – RCP8.5	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in millimeters
Mean temperature in the warmest quarter (1961–1990)	Continuous	Dynamic	https://charcoal2.cnre.vt.edu/climate/current/ ; units are in tenths of °C
Mean temperature in the warmest quarter (2060) – RCP6.0	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in tenths of °C
Mean temperature in the warmest quarter (2060) – RCP8.5	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in tenths of °C
Mean temperature in the coldest quarter (1961–1990)	Continuous	Dynamic	https://charcoal2.cnre.vt.edu/climate/current/ ; units are in tenths of °C
Mean temperature in the coldest quarter (2060) – RCP6.0	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in tenths of °C
Mean temperature in the coldest quarter (2060) – RCP8.5	Continuous	Dynamic	http://charcoal2.cnre.vt.edu/climate/future/ ; units are in tenths of °C

Model development

We used training datasets to individually model distributions of eight amphibian species using the machine-learning algorithm, RF, in Salford Predictive Modeler (SPM) version 7 (Salford Systems, Inc., San Diego, CA, USA; www.minitab.com). RF has proven to be very powerful, highly accurate, and widely used in species distribution modeling (Heikkinen et al. 2012). RF uses “bagging”, which withholds samples of training data and predictors for internal model validation, making RF particularly useful for parsing

small datasets without overfitting (Breiman 1996), which is ideal for modeling rare and endangered species (Mi et al. 2017).

For each model, we grew 200–10,000 trees, used a learning-rate of 0.3, and set the minimum number of observations per node to 2. RF is known to systematically favor high-level categorical variables and include them in trees regardless of their relevance for prediction (Couronné et al. 2018). To prevent this, we limited categorical variables to ≤ 8 categories and penalized other high-level categorical predictors (Landcover: 29 categories; Geology: 63 categories)

by running them as continuous predictors (Hofner et al. 2011).

We assessed model validity using ‘out-of-bag’ (OOB) samples, which RF systematically withholds as an unused portion of the training data, to calibrate the performance of each tree. OOB testing was set to 0.3 (i.e., withholding 30% of training data), except for the Great Plains toad model which had an OOB testing value of 0.1 (10%), Rocky Mountain tailed frog and Plains leopard frog which used 0.4 (40%). We used OOB data (i.e., OOB testing data) to create a receiver operator characteristic (ROC) curve and to calculate the area under the curve (AUC), providing percentages of correctly predicted presences and absences for each model. We used RF to rank the relative importance of predictors to identify those most influential in amphibian SDM models. We also constructed partial dependence plots (PDPs) using R in RStudio and the *pdp* package (Greenwell 2017) to identify response thresholds and non-linear relationships between amphibian occurrence and predictors.

To create baseline (2005) and future (2060) predictions of amphibian distributions, we scored models to a regular lattice of points (1 km resolution), attributed with the same predictors as the training data. Models predicted the relative index of occurrence ($0 < \text{RIO} < 1$) at each point in the lattice (Pearce and Ferrier 2000). RIO values were then smoothed using the *Inverse Distance Weighting* tool in ArcMap 10.5 to generate raster maps for the UMRB. We used 2005 to represent the baseline time period due to the lack of a more recent landcover dataset for the UMRB. Static predictors (i.e., those expected to undergo little change between 2005 and 2060) were held constant for both the 2005 and 2060 models, whereas dynamic predictors (i.e., those expected to change substantially, e.g., climate and land use) were updated for the 2060 models (Table 1). We used two future climate/land-use change scenarios consisting of CMIP5 (Coupled Model Intercomparison Project Phase 5) climatic scenarios (RCP6.0 and RCP8.5) and FORE-SCE land-use/land-change scenarios (B2 and A2) for the UMRB (Sohl et al. 2018). We chose climate scenarios to reflect variable responses including medium (RCP 6.0) and high (RCP 8.5) greenhouse gas emissions, temperature increases, agricultural change, expansion of biomass fuel, and emphasis on environmental

conservation. We paired the RCP 6.0 climate scenario with the CONUS FORE-SCE B2 land-use/land-change scenario, which focuses on environmental and social equity at regional levels, while emissions continue to grow slowly and surface temperature is expected to increase by an average 1.8 °C (IPCC 2007; van Vuuren et al. 2011). We paired the RCP8.5 climate scenario with the CONUS FORE-SCE A2 land-use/land-change scenario to simulate the current atmospheric trajectory; a scenario with an average 2.2 °C increase in global surface temperature resulting from aggressive fossil fuel use and steadily increasing CO₂ emissions caused by changes in land use (IPCC 2007; van Vuuren et al. 2011).

Model validation

To validate the spatial predictive accuracy of the 2005 models, we used independent datasets, composed of georeferenced, presence-only points obtained from HerpMapper, research-grade iNaturalist records, and independent fieldwork datasets (Table 2). In ArcMap 10.5 we calculated the percentage of correctly predicted independent validation points for each model using a symmetric threshold (RIO=0.5) to differentiate between presence and absence points predicted by the model ($< 0.5 = \text{absence}, > 0.5 = \text{presence}$). We used the ‘balanced’ feature in SPM to determine the lowest percentage of misclassification for each model, which was 0.5 for all models. We also compared our model predictions to previously published distribution maps from the primary literature to further evaluate the accuracy of our model predictions.

Analyses

To calculate the change in distribution for each species over time, we reclassified baseline and future model rasters to binary rasters using the 0.5 threshold and the *Reclassify* tool in ArcMap 10.5. This provided the total area (km²) of each species distribution as predicted by the baseline and future models. We then calculated the net change (km²) and percent change in occupied area between the baseline and future models by dividing the net change by the presence area for 2005 for each species. We identified important predictors as those with > 60% relative importance in each species model.

Table 2 Modeled amphibian species with common and scientific names, number of presence and pseudo-absences used to train models, resultant area under the receiver operator characteristic (AUC ROC; 0–1), % of correctly classified presences

(specificity), % of correctly classified absences (sensitivity), overall accuracy (%), number of independent validation presences used to confirm spatial accuracy, and the % of correctly identified presences following spatial validation

Common name	Scientific name	Presences (<i>n</i>)	Pseudo-absences (<i>n</i>)	AUC ROC	Specificity (%)	Sensitivity (%)	Accuracy (%)	Validation (<i>n</i>)	Validation accuracy (%)
Blanchard's cricket frog	<i>Acris blanchardi</i>	139	5,861	0.99	96.9	100	100	76	100
American toad	<i>Anaxyrus americanus</i>	101	3,989	0.99	94.6	100	94.8	29	100
Western toad	<i>Anaxyrus boreas</i>	1,015	5,149	0.99	92.1	97.5	92.9	29	89.7
Great Plains toad	<i>Anaxyrus cognatus</i>	546	1,032	0.89	79.8	80.6	80.6	53	92.5
Woodhouse's toad	<i>Anaxyrus woodhousii</i>	276	866	0.94	84.4	85.7	84.7	22	90.9
Rocky Mountain tailed frog	<i>Ascaphus montanus</i>	122	3,354	0.99	92.8	100	93.1	8	100
Plains leopard frog	<i>Rana [Lithobates] blairi</i>	87	2,627	0.99	96.6	97.4	96.6	23	100
Columbia spotted frog	<i>Rana luteiventris</i>	2,108	13,247	0.99	92.7	98.8	93.5	58	100

Results

Model performance

Baseline model predictions were highly accurate as evidenced by high AUC ROC values which exceeded 89% correct for all species. The Blanchard's cricket frog model was the most accurate, followed by models for American toads, Plains leopard frogs, Rocky Mountain tailed frogs, Columbia spotted frogs, Western toads, Woodhouse's toads, and Great Plains toads (Table 2). Comparisons between predicted baseline distributions and independent validation data points also demonstrated the high spatial predictive accuracy of all models (89.7–100%; Table 2).

Baseline Distributions

Distribution models for Blanchard's cricket frogs, Plains leopard frogs, and American toads had baseline distributions that primarily covered the southeastern

portion of the UMRB. Specifically, there was high overlap between Blanchard's cricket frog and Plains leopard frog baseline distributions, in which both species largely occupied southeastern South Dakota and northeastern Nebraska (Fig. 2). In contrast, American toads encompassed areas east of the James River in South Dakota and the southwestern corner of Minnesota (Fig. 2). Woodhouse's toads and Great Plains toads had widespread distributions throughout the UMRB and baseline distributions predicted these species to be located along the Missouri River (SD, ND, MT) and its tributaries, including the James River (SD), Vermillion River (SD), Big Sioux River (SD), and Yellowstone River (MT; Fig. 2). Western toads, Columbia spotted frogs, and Rocky Mountain tailed frogs inhabited the western edge of the UMRB. The Western toad and Columbia spotted frog distributions spanned areas of Montana and Wyoming (Fig. 3), whereas the Rocky Mountain tailed frog was found only in Montana (Fig. 3).

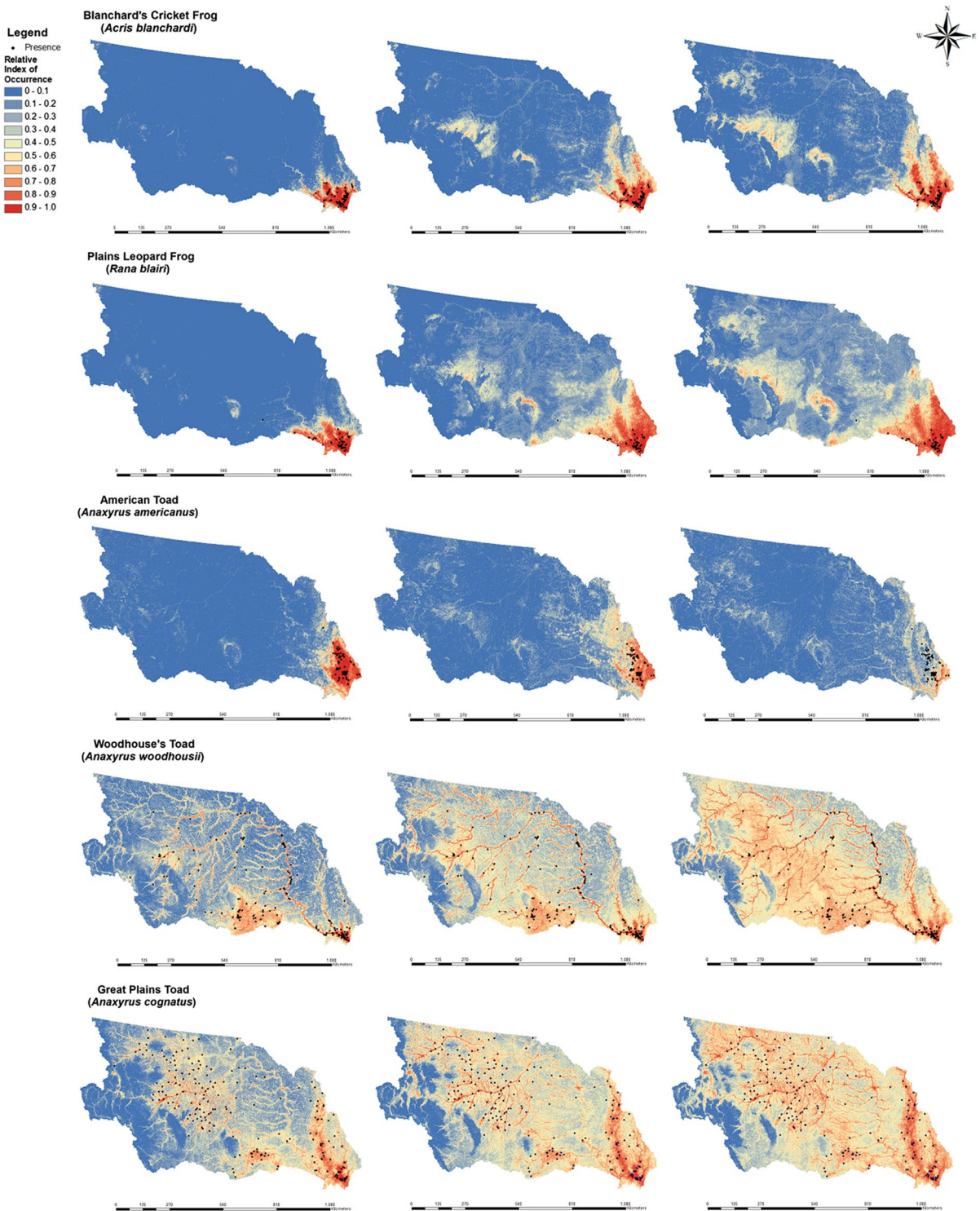


Fig. 2 Predicted relative index of occurrence (RIO) for eastern amphibian species in the Upper Missouri River Basin under baseline (2005) climate and land-use conditions (Col-

umn 1), RCP6.0/CONUS B2 Scenario (2060) (Column 2), and RCP8.5/CONUS A2 Scenario (2060) (Column 3). Black points represent known occurrences

Relative predictor importance

The relative importance of predictors varied among species models (Table 3). We found that climatic and geographic predictors were more influential than anthropogenic predictors for most species. The most important predictors included: mean temperature in the warmest quarter (7 species), elevation (7 species), winter precipitation (4 species), summer precipitation (3 species), geology (3 species), and river distance (2 species). Variable importance also differed by geography, in that species inhabiting the western portion of the study area were highly influenced by mean temperature in the warmest quarter and winter precipitation, whereas species in the eastern UMRB were most influenced by

spring and summer precipitation. Mean temperature in the warmest quarter appeared among the top 4 most important variables for all species, except American toads. PDPs indicated that western species (i.e., Western toads, Columbia spotted frogs, and Rocky Mountain tailed frogs) were detected in areas where mean temperature in the warmest quarter was approximately 15–20 °C, with increasing potential of occurrence at higher temperatures (Fig. 4). PDPs for eastern species (i.e., Blanchard’s cricket frogs and Plains leopard frogs) and toads (i.e., Woodhouse’s toad and Great Plains toads) indicated that these species were found in warmer areas where temperature of the warmest quarter ranged from approximately 23–25 °C, with decreasing potential of occurrence with warmer temperatures (Fig. 4). American toads

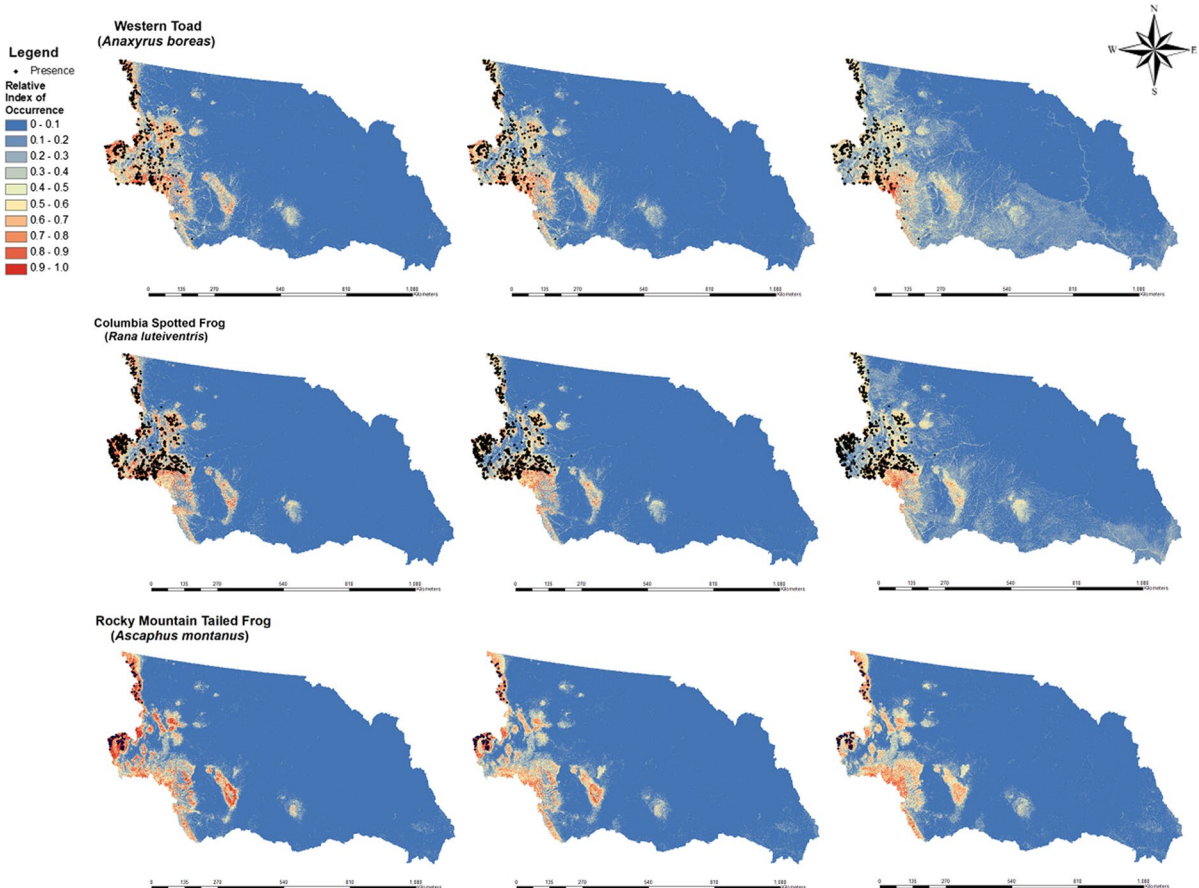


Fig. 3 Predicted relative index of occurrence (RIO) for western amphibian species in the Upper Missouri River Basin under baseline (2005) climate and land use (Column

1), RCP6.0/CONUS B2 Scenario (2060) (Column 2), and RCP8.5/CONUS A2 Scenario (2060) (Column 3). Black points represent known occurrences

Table 3 List of ordered variable importance and relative importance (%) for each species modeled. Only predictors > 60.0% are included

Species	Order of importance	Variable	Relative importance (%)
<i>Eastern species</i>			
Blanchard's cricket frog	1	Summer precipitation	100
	2	Elevation	97.55
	3	Spring precipitation	79.27
	4	Mean temperature in the warmest quarter	62.16
Plains leopard frog	1	Summer precipitation	100
	2	Spring precipitation	86.49
	3	Mean temperature in the warmest quarter	78.71
	4	Elevation	75.29
American toad	1	Summer precipitation	100
	2	Elevation	71.1
	3	Spring precipitation	67.64
Woodhouse's toad	1	River distance	100
	2	Mean temperature in the warmest quarter	70.22
	3	Lake distance	62.76
Great Plains toad	1	Elevation	100
	2	Mean temperature in the warmest quarter	92.37
	3	River distance	65.27
<i>Western species</i>			
Western toad	1	Summer temperature	100
	2	Geology	82.57
	3	Elevation	74.92
	4	Winter precipitation	64.15
Columbia spotted frog	1	Mean temperature in the warmest quarter	100
	2	Elevation	89.25
	3	Winter precipitation	60.39
Rocky Mountain tailed frog	1	Mean temperature in the warmest quarter	100
	2	Elevation	83.07
	3	Winter precipitation	74.94

had a similar response to mean temperature in the warmest quarter, however, this species was primarily detected when temperatures were near 22 °C (Fig. 4). Directional responses for spring and summer precipitation were similar among Blanchard's cricket frogs, Plains leopard frogs, and American toads and indicated a decreasing potential for occurrence in areas with spring rainfall greater than 150 mm (Online Resources 2–3 in Supplemental Material). Winter precipitation response followed a trend similar to other seasons for Western toads, Columbia spotted frogs, and Rocky Mountain tailed frogs (Fig. 5). American toads were associated with the smallest range of winter precipitation (~55–70 mm) and

their response closely resembled that of Blanchard's cricket frogs (Fig. 4).

Predicted changes in distribution

We developed models for two future climatic/land use change scenarios for each of eight amphibian species, generating a total of 16 future models for 2060. Eastern species were predicted to experience varying degrees of expansion under the RCP6.0/CONUS B2 scenario, whereas all montane species were predicted to experience declines (Fig. 3). Distribution changes (i.e., gains and losses) were larger for nearly all species under the RCP8.5/CONUS A2

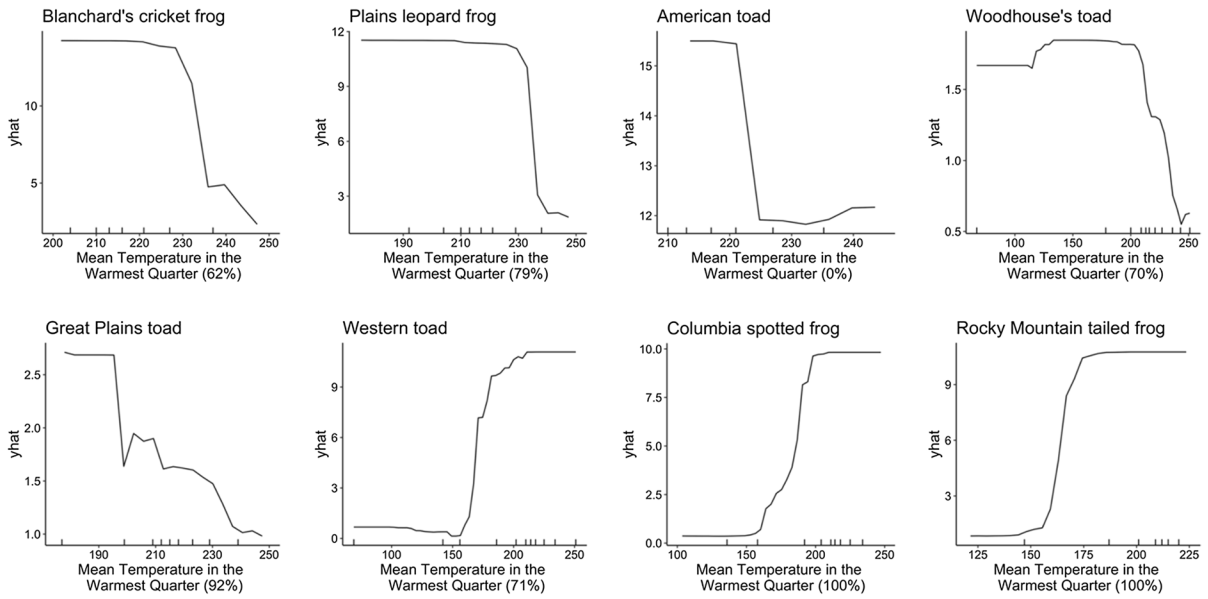


Fig. 4 Partial dependence plots depicting the influence of mean temperature in the warmest quarter (°C×10) for Blanchard’s cricket frogs, Plains leopard frogs, American toads,

Woodhouse’s toads, Great Plains toads, Western toads, Columbia spotted frogs, and Rocky Mountain tailed frogs. The y-axis represents yhat, which is the predicted value

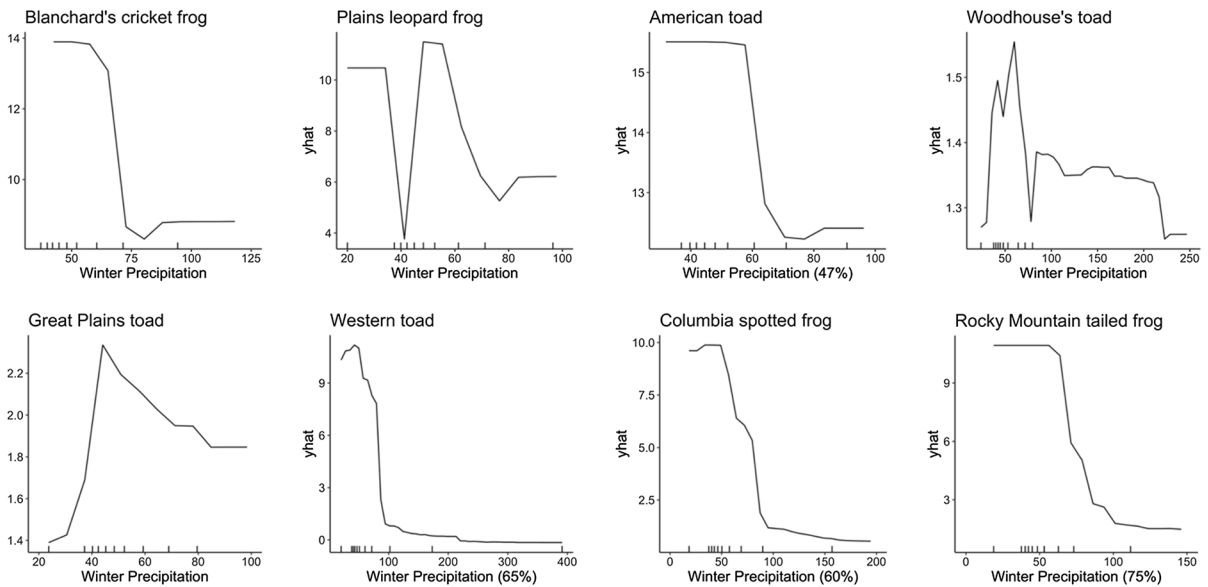


Fig. 5 Partial dependence plots depicting the influence of winter precipitation (mm) for Blanchard’s cricket frogs, Plains leopard frogs, American toads, Great Plains toads, Wood-

house’s toads, Columbia spotted frogs, Western toads, and Rocky Mountain tailed frogs. The y-axis represents yhat, which is the predicted value

scenario compared to the RCP6.0/CONUS B2 scenario. Specifically, Plains leopard frogs and Woodhouse’s toads were predicted to undergo the

largest expansions in occupied area with distribution increases of 238.9% and 243.9%, respectively under the RCP8.5/CONUS A2 scenario (Table 4).

American toads were predicted to experience small gains (8.4% increase) in distribution under the ‘moderate’ RCP6.0/CONUS B2 scenario, however they were also predicted to undergo the largest decline among all modeled amphibian species under the RCP8.5/CONUS A2 scenario (68.4% decline; Table 4). Declines in occupied area mainly affected montane amphibian species (i.e., Columbia spotted frog, Western toad, and Rocky Mountain tailed frog). Additionally, toads (i.e., American toads and Western toads) were predicted to experience larger declines under the RCP8.5/CONUS A2 scenario than the modeled montane anuran species (i.e., Rocky Mountain tailed frogs and Columbia spotted frogs).

All montane species (i.e., Western toads, Rocky Mountain tailed frogs, and Columbia spotted frogs) had high degrees of spatial overlap among distributions. However, under both future scenarios, Western toads and Columbia spotted frogs were predicted to experience larger declines than Rocky Mountain tailed frogs, with their remaining populations confined to the area around Yellowstone National Park, despite an expansion of low-quality areas (e.g., $0 > RIO > 0.1$ in the central UMRB). Specifically, Columbia spotted frogs and Western toads were predicted to experience 27.4% and 36.9% declines in occupied area, respectively, under

the RCP8.5/CONUS A2 scenario. Conversely, the RCP8.5/CONUS A2 model for the Rocky Mountain tailed frog predicted a 9.5% decline in distribution (Table 4).

Elevation was also a top predictor for all species and PDPs indicated eastern species (i.e., Blanchard’s cricket frogs, Plains leopard frogs, and American toads) were detected at elevations of ~350–750 m, with increasing potential of occurrence at higher elevations within their respective ranges (Fig. 6). Woodhouse’s toad and Great Plains toad occurrence was positively correlated with elevation and were found at between ~350 and ~1,500 m (Fig. 6). All three western species (i.e., Western toads, Columbia spotted frogs, and Rocky Mountain tailed frogs) were found between ~1,000 m and ~1,500 m, with decreasing potential of occurrence at elevations higher than 1,500 m (Fig. 6). Geology tended to be more important for amphibian species commonly found at higher elevations (Online Resources 4–5 in Supplemental Material). Anthropogenic factors had less influence on amphibian distributions, although several human-related predictors were among the top five for some species. For example, landcover had a slight influence on American toads (relative importance=42.28%) and Rocky Mountain tailed frogs (relative importance=31.81%; Online Resources 6–7

Table 4 Predicted area of presence (km²) for each modeled amphibian species in the Upper Missouri River Basin. Net change between baseline and future scenarios was calculated

by subtracting the presence area of the future scenario in 2060 from the presence area in 2005. Percent change is the net change divided by the respective presence area in 2005

Species	Presence area 2005	Presence area 2060 RCP6.0/B2	Net change 2060 RCP6.0/B2	% Change 2060 RCP6.0/B2	Presence area 2060 RCP8.5/A2	Net change 2060 RCP8.5/A2	% Change 2060 RCP8.5/A2
Blanchard’s cricket frog	22,614	47,097	24,483	108.3%	62,807	40,193	177.7%
Plains leopard frog	27,200	69,252	42,052	154.6%	92,169	64,969	238.9%
American toad	39,036	42,312	3,276	8.4%	12,324	-26,712	-68.4%
Woodhouse’s toad	120,954	203,921	82,967	68.6%	416,010	295,056	243.9%
Great Plains toad	176,650	260,806	84,156	47.6%	359,560	182,910	103.5%
Western toad	55,980	42,845	-13,135	-23.5%	35,342	-20,638	-36.9%
Columbia spotted frog	55,050	42,392	-12,658	-23.0%	39,948	-15,102	-27.4%
Rocky Mountain tailed frog	49,666	43,657	-6,009	-12.1%	44,967	-4,699	-9.5%

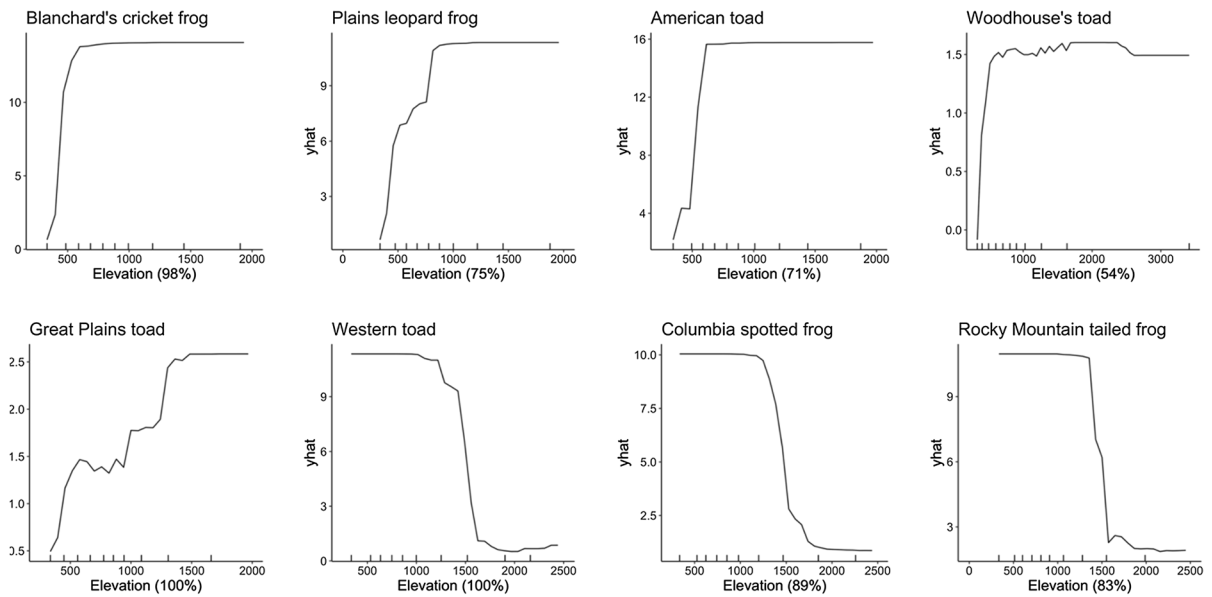


Fig. 6 Partial dependence plots depicting the influence of elevation (m) for Blanchard's cricket frogs, Plains leopard frogs, American toads, Woodhouse's toads, Great Plains toads, West-

ern toads, Columbia spotted frogs, and Rocky Mountain tailed frogs. The y-axis represents \hat{y} , which is the predicted value

in Supplemental Material). Additionally, distance to pollution was the fourth most influential variable for Great Plains toad distribution (relative importance=55.26%; Online Resource 8 in Supplemental Material).

Discussion

Distributions of four eastern amphibian species were predicted to expand under both future climatic and land-use/change predictions (RCP6.0/CONUS B2 and RCP8.5/CONUS A2), whereas distributions for one eastern species (i.e., American toads) were predicted to experience opposite effects under the two future scenarios. All eastern species had similar responses to spring and summer precipitation and were positively associated with values as high as 125 mm during each season. This likely reflects the life histories of these species and their need for permanent and semi-permanent bodies of water for reproduction in spring and summer (Anderson et al. 1999; Grant et al. 2015; Badje et al. 2021). Conversely, amphibian species inhabiting the western portion of the study area were predicted to experience distribution declines but were associated with mean temperatures

during the warmest quarter between 15 and 20 °C and negatively impacted when winter precipitation exceeded 50 mm. The strong association with mean temperature in the warmest quarter could reflect these cold-adapted species' dependence on growing season length and specific water temperatures (Metter 1964; Claussen 1973; Pilliod et al. 2022), whereas the association with winter precipitation (i.e., snow at higher elevations) likely reflects their need for adequate snowpack insulation to prevent montane streams from freezing and the resulting snowmelt to replenish montane water resources (e.g., breeding wetlands Dupuis et al. 2000; Ray et al. 2016).

Amphibians in eastern UMRB

The southeastern corner of the UMRB represents the northernmost suitable habitat for Blanchard's cricket frogs and Plains leopard frogs, with cold winter temperatures limiting northward dispersal (Lynch 1978; McCallum and Trauth 2004). As temperature and precipitation levels increase in this area, both species are predicted to experience a northward shift and an overall increase in distribution. Recent studies have documented that Blanchard's cricket frogs use rivers and streams for overwintering in southwestern

Wisconsin (Badje et al. 2016, 2021). Spring migration patterns typically occur along riparian systems, effectively connecting overwintering habitat to breeding wetlands. Summer precipitation was the most important predictor for Blanchard's cricket frogs and Plains leopard frogs, suggesting these species may benefit from a wetter environment during the breeding season. Notably, our model shows that, in response to increased temperatures and precipitation, there is potential for Plains leopard frogs to spill over into the southeastern corner of Minnesota, which is not a part of their present-day distribution. Despite positive predictions for Blanchard's cricket frog and Plains leopard frog distributions, both species are currently listed as 'species of concern' in South Dakota and should continue to be monitored (Fischer et al. 1999).

The two toad species that occupy the eastern UMRB (i.e., Great Plains toads and Woodhouse's toads), were also predicted to experience increases in distribution area under both scenarios. Elevation was the most important predictor for Great Plains toads, while distance to rivers was the most influential predictor for Woodhouse's toads. Great Plains toads appear to disperse via river pathways or floodplains and mainly breed in temporary pools filled by rainwater when temperatures exceed 12 °C (Bragg 1940), so we believe elevation may serve as a proxy for the interaction between climatic variables (i.e., cooler temperatures and more precipitation). Mean temperature in the warmest quarter also had a large influence on this species' distribution, which is unsurprising since Great Plains toad tadpoles tend to congregate in shallow water where warmer temperatures allow them to develop faster (Hansen et al. 2012). However, warmer summer temperatures could also hinder Great Plains toads, as breeding pools could evaporate before tadpoles can complete metamorphosis. Previous studies have also shown that this species is heavily dependent on agricultural wetlands (Mushet et al. 2012), which tend to have higher levels of pollution (Blann et al. 2009; Campbell et al. 2023). This is consistent with our results that indicate a positive relationship between distance to pollution and Great Plains toad occurrence.

The distribution of Woodhouse's toads along the Missouri and Yellowstone Rivers was highly influenced by their proximity to rivers and lakes in the model. Woodhouse's toads are known to occur in

high-density, temporary wetland landscapes (Lannoo 2005) and overwinter near deep-water habitat as they are not a freeze-tolerant species (Swanson et al. 1996). Our results are consistent with previous research indicating that distance to deep water strongly influenced habitat suitability for Woodhouse's toads (Mushet et al. 2012). Woodhouse's toad occurrence was also strongly influenced by mean temperature in the warmest quarter between 10 and 25 °C. Our findings mirrored those of Johnson and Batie (2001), in which Woodhouse's toads in North Dakota were detected at temperatures of approximately 12 to 25 °C and were most active at temperatures between 18 and 21 °C.

Unlike models for the other toad species, the RCP6.0/CONUS B2 model predicted small distribution gains for American toads in eastern South Dakota, whereas the RCP8.5/CONUS A2 model predicted pronounced declines for this species. The RCP6.0/CONUS B2 scenario represents a situation with modest climate change and shifts in land use to accommodate BECCS. Specifically, grassland and wetland classes are expected to increase to some degree under this scenario, whereas the amount of area used for cropland is predicted to decrease (Sohl et al. 2014). Given the importance of precipitation in our American toad model, increases in wetland and grassland habitat under the CONUS B2 scenario should aid American toad persistence. American toads require permanent or ephemeral bodies of water for reproduction and prefer open deciduous forests or grassland habitat as adults (Dodd 2013). Low-intensity agriculture and increased deciduous forest cover, conditions embodied by the CONUS B2 land-use/change scenario (Sohl et al. 2014), have also been associated with American toad persistence (Gibbs et al. 2005). Conversely, the CONUS A2 land-use/change scenario represents a future with substantial wetland and grassland loss and a 7.8% increase in cropland from 2010 to 2050 (Sohl et al. 2014). Although adults are relatively tolerant of arid conditions, American toad tadpoles require hydroperiods longer than 6 – 8 weeks to complete metamorphosis (Oldfield and Moriarty 1994). Prairie pothole wetlands are highly dependent on snow melt (i.e., winter precipitation) and spring precipitation to maintain their ephemeral status and will be influenced by precipitation changes in the future. Despite predicted increases in precipitation in the

eastern UMRB, increased rainfall may not outweigh projected increases in temperature, resulting in reduced hydroperiod and water loss for wetlands (Fay et al. 2016), likely affecting the survival of American toad tadpoles and juveniles. This scenario also represents a 50.5% increase in urban area (Sohl et al. 2014), which has been negatively associated with American toad occurrence and may play a role in the disappearance of this species under the CONUS A2 scenario (Gibbs et al. 2005).

Amphibians in western UMRB

In contrast to the low-elevation, grassland, and agricultural areas of the eastern UMRB, the western portion of the UMRB includes high elevation, forested areas in Montana and Wyoming. Our models predicted that Columbia spotted frogs and Western toads would undergo larger declines compared to Mountain Rocky tailed frogs. Western toads are listed as a species of concern in Wyoming (Franklin et al. 2018) and Montana, whereas Columbia spotted frogs are currently listed as a sensitive species by the United States Department of Agriculture (USDA) Forest Service in Region 2 (USDA Forest Service 2023). Surprisingly, Columbia spotted frogs are listed as 'Least Concern' by the International Union for Conservation of Nature (IUCN), despite their USDA listing and previous reports of population declines resulting from substantial changes in climatic and hydrologic conditions (McMenamin et al. 2008). Alternatively, Rocky Mountain tailed frogs are not a species of concern in Wyoming or Montana and are listed as 'Least Concern' by the IUCN (IUCNredlist.org).

The distributions of these three western species overlapped substantially with one another and had the same top predictors (i.e., mean temperature in the warmest quarter, elevation, winter precipitation levels, and geology), albeit in different orders of importance. These four variables interacted to predict species distributions, in which elevation is linked to temperature during summer and winter months, winter precipitation dictates snowfall, and geology influences soil moisture content, bedform stability, and pore-space refugia (Jiang et al. 2020). Columbia spotted frogs were predicted to experience declines in occupied areas (23.0% decline) under the RCP6.0/CONUS B2 scenario, however these declines were

higher (27.4%) under the warmer, agriculturally intensive RCP8.5/CONUS A2 scenario. This difference suggests that Columbia spotted frogs are impacted by changes in land conversion, with substantially lower mean RIO values in agricultural (RCP6.0/CONUS B2 RIO=0.11; RCP8.5/CONUS A2 RIO=0.04) versus forested areas (RCP6.0/CONUS B2 RIO=0.40; RCP8.5/CONUS A2 RIO=0.39). Although changes in land use may directly impact available habitat, it is also plausible that an increase in agricultural activity coupled with elevated summer temperatures could result in higher water withdrawals thereby decreasing riparian water flow and availability (Allan et al. 2021). Notably, the model generalized well, accurately predicting the presence of Columbia spotted frogs in Wyoming's Great Divide Basin, despite not being trained with occurrence records from this region due to lack of available occurrence data. Our models are consistent with previous studies that indicated the disjunct Great Divide Basin population of Columbia spotted frogs may not persist under the RCP8.5/CONUS A2 scenario as a result of declining habitat due to warmer and drier conditions, the effects of which may be compounded by geographic and genetic isolation (Arkle and Pilliod 2015; Pilliod et al. 2015).

Interestingly, Rocky Mountain tailed frogs were predicted to undergo larger declines under the RCP6.0/CONUS B2 scenario compared to the RCP8.5/CONUS A2 scenario. Under both scenarios, average RIO declined, indicating a reduction montane habitat suitability for this species. Rocky Mountain tailed frogs typically reside in and next to mid- to high-elevation cold-water mountain streams within old growth forests (Dupuis and Friele 2006). This was supported by our model, as indicated by the high relative importance of elevation. Our results are also consistent with previous research indicating the importance of geology and land-use in determining the occurrence of Rocky Mountain tailed frogs (Dupuis and Friele 2006). Changes in land use, such as clearcut logging and reforestation, are expected to increase under the RCP6.0/CONUS B2 scenario due to a focus on self-reliance and the use of local resources (Sohl et al. 2014). Logging can decrease overhead canopy cover and result in the warming of headwater streams and reduced soil moisture, whereas reforestation results in a lower mean forest age and less canopy cover. Adult Rocky Mountain tailed frogs

are very small (~25 – 50 mm) and have low thermal and desiccation tolerances, thus decreased canopy cover and increased sun exposure may alter Rocky Mountain tailed frog population dynamics. Alternatively, clearcut logging can increase flooding and promote sediment transport to nearby streams, which may further impact local populations, especially since Rocky Mountain tailed frogs use streams for breeding and they have a primitive hopping ability that limits dispersal (Hobbs et al. 2019), and long generation times that slow population recovery following disturbance (Halofsky et al. 2018).

Among the three montane species, Western toads were predicted to experience the largest declines under both future scenarios. Western toad survivorship has been linked to snow depth and winter environmental moisture levels in Colorado (Browne and Paszkowski 2010), which is consistent with our results highlighting the importance of winter precipitation, elevation, and geology in Western toad occurrence. Western toads, along with the other two montane amphibian species, are freeze intolerant and so require sufficient overwintering habitat (i.e., deep snow and high winter moisture levels; Scherer et al. 2008). Occurrence was negatively correlated with winter temperature, winter precipitation, and elevation in our model, which suggests amphibian populations may need to migrate to higher elevations in search of suitable hibernacula. Although a warming climate with milder winters may be physiologically beneficial for these freeze intolerant, montane species (McCaffery and Maxell 2010), such climatic conditions could also contribute to the desiccation of vital aquatic habitat and poor insulation of hibernacula. Moreover, warmer winters may allow for the growth of the pathogenic fungus, *Batrachochytrium dendrobatidis* (*Bd*), which has an optimal temperature range of 4 – 25 °C (Piotrowski et al. 2004). Winter temperatures within this range could contribute to increased infection and mortality rates in Western toad populations during a time of the year when they should be ‘safe’ from this deadly pathogen. Given the anticipated increase in prevalence of disease and the drying and warming effects of climate change in the western UMRB, it seems likely that montane amphibian populations and their occupied habitat will continue to decline as predicted by our models.

Conclusion

Overall, future changes in amphibian distributions were highly variable by species and geography. Although all species were predicted to experience localized changes in occurrence, future predictions indicate that montane species are at the highest risk of population declines. Anurans, that primarily occurred in lowlands and grasslands (i.e., eastern amphibian species), were at the lowest risk of declines, and were predicted to experience distribution expansions by our models. Amphibians in the western portion of the UMRB will likely suffer as a result of increased temperatures and shallower snow-packs, that may lead to the drying of mountain streams and wetlands. These conditions were more intense under the RCP8.5 climate scenario, resulting in more pronounced declines in distribution area in the mountainous, western UMRB. However, these montane species primarily occupy high elevation sites and are therefore less likely to be directly impacted by high-intensity agriculture.

In contrast, amphibians distributed across the eastern UMRB were generally predicted to experience future increases in occupied area (except American toads). These species stand to benefit from increased temperatures and precipitation, which may provide new thermally suitable habitat, allowing for northward range expansion, particularly under the RCP8.5 climate scenario. Alternatively, agricultural intensification and subsequent decreased grassland and wetland habitat may restrict expansion of American toads in the region at smaller scales. Amphibians in the eastern UMRB are highly dependent on aquatic habitat (i.e., wetlands, rivers, lakes), so increased agricultural production and urbanization that contribute to higher pollution levels may inhibit distributions of species in remaining aquatic habitats.

Analogous research predicted many grassland bird species in the UMRB to benefit from a warming climate (Baltensperger et al. 2020), however the impacts of climate change are likely to be more severe for amphibian populations due to their moisture sensitivity and inability to disperse long distances in search of suitable habitat. Similarly, climatic predictors were expected to have a larger impact on grassland bird distributions compared to land-use variables (Baltensperger et al. 2020), which is consistent with our amphibian models. Although we were unable to

model the direct impacts of BECCs on amphibian distributions, most of the modeled species were only minimally affected by land-use variables. Amphibians in the UMRB, particularly in the eastern portion, already exist in a highly modified agricultural landscape with bioenergy crops (e.g., corn [*Zea spp.*], soybean [*Glycine max*], canola [*Brassica napus*], sorghum [*Sorghum spp.*]) and may be less impacted by biofuel cultivation compared to widespread changes in temperature and precipitation levels. Additionally, many of the modeled amphibians in the western UMRB may also be minimally impacted by biofuel land conversion due to their preference for high elevations and areas not suitable for agriculture. However, land managers and amphibian conservationists should closely examine and consider species-specific habits and physiological requirements in addition to habitat connectivity, agricultural pollution levels and implications of BECCs on amphibian habitat when designing conservation strategies. Ultimately, the persistence of amphibian populations in the UMRB will depend on the availability, connectivity, and quality of aquatic habitat as well as the ability of species to adapt to rapidly changing conditions.

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Author contributions All authors contributed to the study conceptualization and implementation. Data collection, analysis, and visualization were performed by KSC. APB gathered and prepared predictor variables, in addition to providing project supervision and guidance. JLK aided in funding acquisition and project administration. The first draft of the manuscript was written by KSC and all authors provided feedback on subsequent versions of the manuscript. All authors read and approved the final version of the manuscript.

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Data availability Data and code can be made available upon request; however, we are restricted from sharing amphibian locational records obtained from the Montana Natural Heritage

Program, South Dakota Natural Heritage Program, and HerpMapper. Species distribution models, environmental predictors, and compiled GBIF datasets can be downloaded at: <https://osf.io/8wu5e/>.

Declarations

Conflict of interest The authors do not have any financial or non-financial interests to disclose.

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