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PREDICTED SUITABLE HABITAT DECLINES FOR MIDWESTERN UNITED STATES AMPHIBIANS UNDER FUTURE CLIMATE CHANGE AND LAND-USE CHANGE SCENARIOS

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Abstract.—With current declines of vertebrate taxa meeting or exceeding those of historic mass extinction events, there is a growing need to investigate the main drivers of losses. Two of the main drivers of declines are global climate and land-use changes, both affecting multiple groups of taxa. Amphibians are at great risk from these two drivers of change and investigations into the impact of future change could assist with the formation of conservation plans to mitigate losses. Forecasting changes in suitable habitat with ecological niche modeling serves as a useful tool to begin to understand how species may respond to anthropogenic change. We used Maxent to model suitable habitat space of 33 amphibian species within the Midwestern U.S. under multiple future climate change scenarios and used current and predicted changes in land-use to examine the predicted impact of global climate and land-use change. We predicted reductions in suitable habitat for a high proportion of species in all model scenarios, while few species were predicted to gain suitable habitat. No significant differences in percentage change in habitat space were determined between models predicting suitable habitat solely using climate change scenarios or model output that incorporated the impact of land-use change. Species richness of amphibians is predicted to decrease based on future climate and climate + land-use scenarios. In the future, we encourage continuation of the examination of land-use and other global stressors, and further investigations into physiological tolerances of amphibian species to create more robust predictions.

Key Words.—bioclimatic variables; climatic niche; distribution shifts; representative concentration pathway; species distribution model.

INTRODUCTION

Many scientists think we are currently undergoing a sixth mass extinction of global taxa, with losses of vertebrate species meeting or exceeding those of historic mass extinction events (Barnosky et al. 2011; Dirzo et al. 2014; Pievani 2014; McCallum 2015). The cause of these predicted and quantified extinctions is most prominently habitat change, global climate change, invasive species, and over-collection, all of which are linked to human activity (Pievani 2014). Two of the primary anthropogenic changes affecting terrestrial vertebrates are land-use and global climate change, each of which have been associated with declines in populations of mammals, birds, reptiles, and amphibians (Bryja et al. 2002; Chace and Walsh 2006; Fahrig and Rytwinski 2009; Delaney et al. 2010; Clipp and Anderson 2014). With a high percentage of land being modified within the past 30 y in the United States (Sleeter et al. 2013), land-use change has become a pervasive problem for conservation biology. Predictions of increased future land-use change in the United States (Radeloff et al. 2012) promotes the need for further study of the impact land-use changes have

on biodiversity. In addition, global climate change is responsible for recent reductions of many vertebrate populations (McCarty 2001; Feehan et al. 2009; Lawler et al. 2009), and is likely to be a significant driver of extinctions in the future (Araujo et al. 2006). Studies examining the predicted synergistic effects of land-use and climate change can help elucidate the impact of change across ecosystems and assist with the formation of conservation plans to mitigate changes or losses.

Amphibians are declining at higher rates compared to other vertebrate classes (except fishes; Stuart et al. 2004; McCallum 2007; Wake and Vredenburg 2008; Collins 2010; Wake 2012). Amphibian population declines have been linked to a variety of factors, such as habitat fragmentation, land-use changes, chemical pollution, climate change, and disease (Taylor et al. 2005; Fahrig and Rytwinski 2009; Todd et al. 2011; Pereira et al. 2013). Land-use characteristics and vegetative structure influence fine-scale microclimates, which are important for amphibians (Peterman and Semlitsch 2014), namely for maintaining physiological requirements. Thus, changes in temperature and precipitation on a fine scale can dramatically alter habitat suitability for amphibians. For example, changes to forest habitat (e.g., forest roads

and clear-cutting) have been found to significantly reduce the abundance of forest-dwelling salamanders in several studies (Petranka et al. 1994; Semlitsch et al. 2007; Homyack and Haas 2009; Hocking et al. 2013; Harper et al. 2015). In addition, amphibians use specific habitats for breeding areas and refuge from predators (Trenham and Shaffer 2005; Scott et al. 2013; Osbourn et al. 2014). Consequently, anthropogenic disturbance of natural habitat has resulted in declines among several amphibian populations (Naughton et al. 2000; Barrett and Guyer 2008; Pillsbury and Miller 2008; Price et al. 2011).

While land-use affects amphibian habitat suitability locally, climate is a critical factor that shapes the suitability of amphibian habitat at local, landscape, and larger geographic scales. Amphibians are poikilothermic and thus rely on their external environment to maintain body functions for survival. In addition, the broader geographic distribution of species is also determined by larger climate regimes, as these broad regimes constitute the make-up of microclimates (Jimenez-Valverde et al. 2011). Global climate change threatens to significantly alter broad climatic regimes that directly shape the distributions of amphibians, therein forcing either their adaptation or migration. Broad shifts in distributions, however, could be problematic for many amphibian species because of their low dispersal abilities (Trenham and Shaffer 2005; Scott et al. 2013; Hillman et al. 2014) and relatively small home ranges (Findlay and Houlihan 1997) compared to other taxa. Therefore, predictions of how climate change and land-use changes may alter the suitability of habitat for amphibians are useful to assist in the creation of management or conservation efforts.

Forecasting changes in suitable habitat with species distribution modeling (SDM) serves as a useful tool to begin to understand how species may respond to anthropogenic change (Pearson and Dawson 2003; Phillips et al. 2006). Doing so for multiple species can uncover how biodiversity and ecosystem processes may change as well. For example, amphibians are important for nutrient cycling and storage within and between ecosystems (Burton and Likens 1975; Regester et al. 2006; Semlitsch et al. 2014; Milanovich et al. 2015; Milanovich et al. 2016). A loss of functional diversity of amphibians could therefore disrupt important ecological processes. Thus, modeling potential changes in amphibian biodiversity is important for understanding potential consequences for these processes. Species distribution modeling has been employed to forecast the effects of climate change on amphibian habitat in recent studies (Milanovich et al. 2010; Barrett et al. 2014; Groff et al. 2014; Fong et al. 2015; Sutton et al. 2015) and these studies predict wide-ranging reductions in suitable habitat for nearly all amphibians under future climate change scenarios. Additionally, many of these

studies find that predicted suitable habitat for species shifted toward areas with higher elevation to follow suitable habitat with predicted climatic changes. This serves the same function as species shifting higher in latitude (Randin et al. 2013), but elevation offers this analogous change in climate over a shorter distance. For amphibians, adjacent climatic refuge may be essential because of their low vagility and their close association with breeding habitats (Semlitsch 2008). Therefore, regions with substantial amphibian diversity and relatively low relief (e.g., the Midwestern United States) may result in significant losses in suitable amphibian habitat. Yet, most amphibian SDM studies have focused on montane regions, potentially buffering their predicted effects (Milanovich et al. 2010; Sutton et al. 2015). In addition, land-use has seldom been included in amphibian SDMs (Thuiller et al. 2004; Hof et al. 2011; Barbet-Massin et al. 2012), although it is widely recognized to be a limiting environmental variable for amphibian habitat.

Our objectives were to use SDMs to predict future effects of predicted global climate and predicted land-use change on the suitable habitat of amphibian species and resulting amphibian species richness in the Midwestern United States. We predict Midwestern amphibians will show a greater reduction in future suitable climatic habitat compared to other studies outside of the Midwestern U.S., and that predictions of suitable habitat reductions will increase through time and with the incorporation of predicted land-use change. Furthermore, we predict amphibian species richness will follow the same pattern and also decrease over time.

MATERIALS AND METHODS

Study area and species.—We used SDMs to project species distributions of amphibians in the Midwestern United States (herein Midwest) based on several global climate change scenarios (herein climate-only models). The Midwest was defined by the boundaries of eight states: Minnesota, Iowa, Missouri, Illinois, Wisconsin, Michigan, Indiana, and Ohio. The majority of our study region is dominated by similar habitats including floodplains, lowland forests, agriculture, and prairies. However, it does contain some small portions of higher elevation habitats such as the Ozark Highlands, portions of the Interior Plateau, and the Western Allegheny Plateau (Fig. 1). We modeled the suitable climatic habitat of 33 amphibian (19 salamander, 14 anuran) species with any portion of their current known distribution within the study area (Appendices A and B). Other species were not included in models for lack of data (< 20 individual point localities). Four of the 33 species included represent species complexes. Complexes were comprised of species that were either

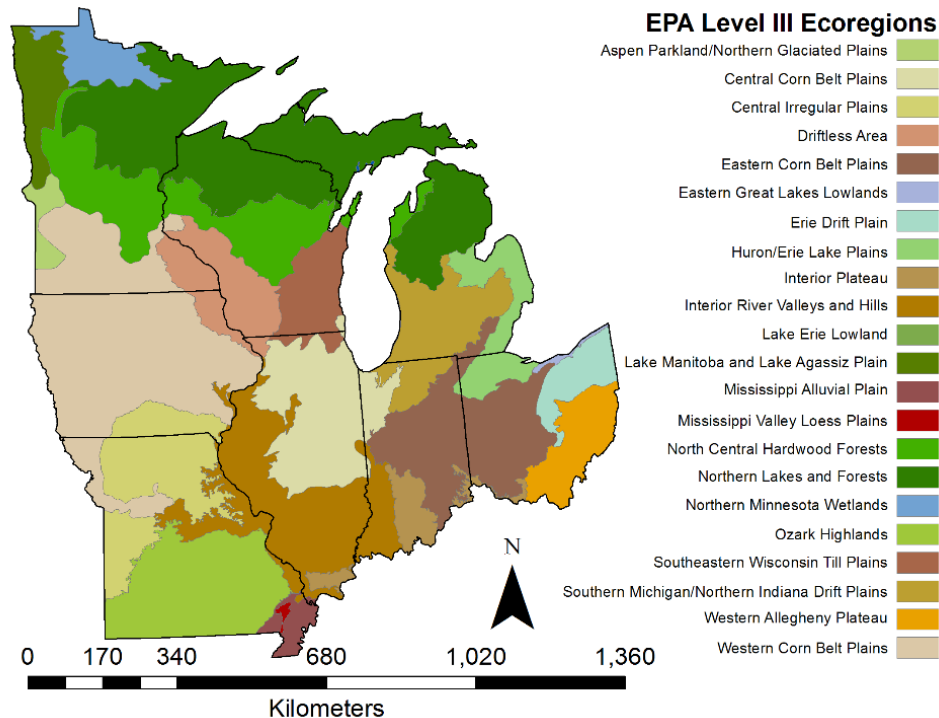


FIGURE 1. The Midwest region of the U.S. (model region) depicted with the U.S. Environmental Protection Agency (EPA) Level III Ecoregions.

two sub-species of the same complex, (*Plethodon glutinosus*/*Plethodon albagula* complex, *Eurycea bislineata*/*Eurycea cirrigera* complex, and *Plethodon cinereus*/*Plethodon serratus* complex), or species that have overlapping ranges and are difficult to differentiate (*Hyla versicolor*/*Hyla chrysoscelis* complex). Species complexes were modeled as a single species. As a result, our study represents 62% of the total number of amphibian species with some portion of their current known distribution within our study region.

Environmental data.—We used four predicted future climate change scenarios from the Intergovernmental Panel on Climate Change (IPCC) 5th Assessment Report (AR5; IPCC 2014) under two global circulation models (GCM; CCSM4 [CCSM] and HadGEM2-ES [Hadley]) and two representative concentration pathway (RCP) greenhouse gas emissions projections, RCP 2.6 (Low) and RCP 8.5 (High), from each GCM, each across three decades: current (average of years 1950–2000), 2050 (average of years 2041–2060) and 2070 (average of years 2061–2080). Each RCP emissions scenario represents changed radiative forcing relative to pre-industrial atmospheric greenhouse gas levels (van Vuuren et al. 2011). The AR5 scenarios (RCPs 2.6, 4.5, 6.0, 8.5) range from anthropogenic greenhouse gas emissions reversal to continued anthropogenic greenhouse gas emissions through the year 2100. The RCP 2.6 scenario

predicts anthropogenic greenhouse gas emissions peak before mid-century and decline thereafter, thus being the lowest predicted emissions scenario. The RCP 8.5 scenario is the highest predicted emissions scenario and predicts continued increased anthropogenic greenhouse gas emissions to the year 2100. We selected global circulation models for our SDMs because of the effectiveness their previous versions in reproducing important Northern Hemisphere oscillations (Stoner et al. 2009), indicating their ability to accurately reproduce natural meteorological phenomenon. We used two separate GCMs and RCP projections to account for potential bias from either predictive model on its own. Additionally, multi-GCM and RCP approaches are commonly used in climate-based SDMs (Milanovich et al. 2010; Matthews et al. 2011; Barbet-Massin et al. 2012; Barrett et al. 2014; Sutton et al. 2015) and the approach to create an ensemble of projections has received support (Araujo and New 2007). Climate data were generated by Hijmans et al. (2005) and downloaded from the WorldClim database (WorldClim. 2005. Free climate data for ecological modeling and GIS. Available from www.worldclim.org [Accessed 20 September 2014]) with 30 arc second resolution (about 1 km²). We used 11 out of 19 bioclimatic variables provided by WorldClim (Fig. 2). We selected bioclimatic variable layers used in models based on previous use in a similar amphibian bioclimatic modeling study (Sutton

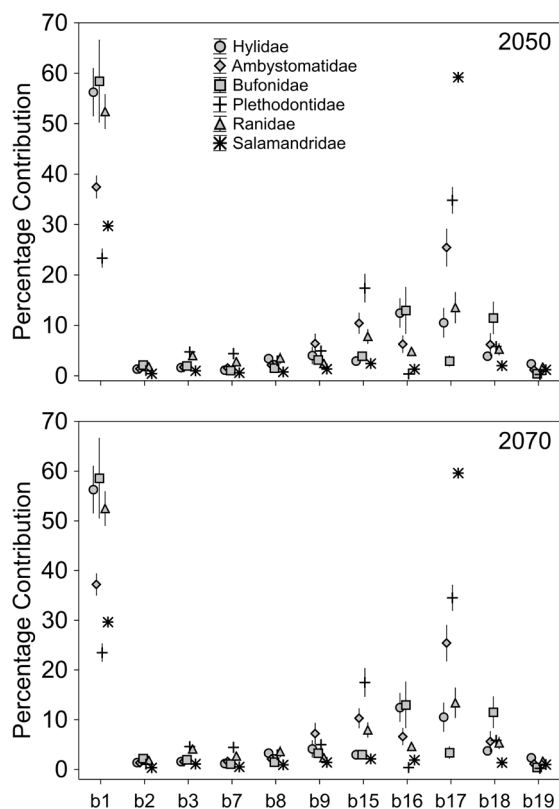


FIGURE 2. Plot of mean (\pm SE) percentage contribution of bioclimatic variables to models by amphibian family for each model decade (2050 and 2070). On X axis, b1 = Annual Mean Temp; b2 = Mean Diurnal Range (Mean of Monthly Max Temp - Min Temp); b3 = Isothermality (Mean Diurnal Range/Min Temp Range) \times 100; b7 = Temperature Annual Range (Max Temp of Warmest Month - Max Temp of Coldest Month); b8 = Mean Temperature of Wettest Quarter; b9 = Mean Temperature of Driest Quarter; b15 = Precipitation Seasonality (Coefficient of Variation); b16 = Precipitation of Wettest Quarter; b17 = Precipitation of Driest Quarter; b18 = Precipitation of Warmest Quarter; b19 = Precipitation of Coldest Quarter.

et al. 2015) in which highly correlated variables were consolidated, which resulted in 11 bioclimatic variables used in models. Although 1 km² is a relatively fine scale for the large study area in which we are focused, we lose the finer-scale variation in environmental data that may be important to our study organisms. This may be especially true for amphibians as habitat suitability is likely influenced not only by broader climate conditions but also microclimates. However, we assume the changes to climate at the resolution of our data will be reflective of the changes in climate at finer scales.

Occurrence data.—Species occurrence data represent geographic locations collected by a variety of sources of documented sightings and were accumulated from the Biodiversity Serving Our Nation (BISON) database (USGS. 2014. Biodiversity Serving our Nation. Available from <https://bison.usgs.gov/#home>

[Accessed 4 October 2014]) and the HerpNet database (HerpNet, Global Biodiversity Information Facility, and the National Science Foundation. 2014. Available from www.herpnet.org [Accessed 4 October 2014]). These data are compiled by several natural history museums and are either specimens that have coordinates associated with them or localities where specimens have been found by trusted experts. We discarded coordinates of each datum point if there were less than four digits after the decimal to ensure accuracy within the resolution of our environmental data (1 km²). Supplementary to that, we filtered data in ArcMap™ version 10.2 to only include occurrence data within their respective current known distribution according to county-based range maps of the National Amphibian Atlas of the U.S. Geological Service (Lannoo 2005) and International Union for the Conservation of Nature (IUCN) range maps (NatureServe and IUCN. 2016. Spatial Data Download. Available from <http://www.iucnredlist.org/technical-documents/spatial-data> [Accessed 18 July 2016]) to exclude potential misidentifications or points in locations where a species is no longer found. We used the entire species current known distribution to model their total climatic niche. We chose 10,000 background samples at random within the current known distribution of each species to sample pseudo-absences to build models. Using only occurrence data without known absences can potentially bias our models. Selecting randomly placed pseudo-absences in the species ranges may not necessarily reflect the localities and climate in which a species does not occur. However, we sought to address this bias by using the null model approach.

Maxent modeling.—We performed projected current and future distributions of amphibians for climate-only models using Maxent version 3.3.3k. We modeled the entire currently known distribution across North America for each of the 33 study species. Maxent is an ecological niche modeling program that uses presence-only points in concert with continuous environmental raster data to determine the current ecological niche for each input species (Phillips et al. 2006). Predicted projections of future suitable habitat are made with Maxent by providing forecasted layers of the environmental data. Maxent then projects future predicted suitable habitat derived from environmental forecasts referencing current niches that it has determined. Since its introduction, Maxent has been used increasingly to model species distributions with presence-only data and there is a growing body of evidence on its superior accuracy to other presence-only modeling applications (Phillips et al. 2006; Merow et al. 2013).

Sampling bias is a well-known limitation of presence-only occurrence data because they are often a

collection of datum from multiple sources likely with varying sampling efforts (Ruiz-Gutierrez and Zipkin 2011). Therefore it is difficult to distinguish areas with a high density of individuals between areas sampled with higher sampling effort or areas better represented from heavier sampling frequency (e.g., an ecological research site). We accounted for this inherent bias by thinning data points within a 5-km radius of one another with the Spatial Rarify tool in the SDM Toolbox add-in (Brown 2014) for ArcMap. This distance is effective in eliminating spatial autocorrelation within heavily sampled areas for amphibians (Barrett et al. 2014), improving model accuracy.

Projecting future species suitable climatic habitat.—

For creation of climate-only SDMs, we built an ensemble model design to create a gradient of predictions to reduce influence of single modeling variables. We used a replicate runs approach with 10 replicate runs for each modeling scenario to obtain an average of model runs in Maxent. As described above, we created our SDMs for three decades (current, 2050, and 2070), two GCMs (CCSM4 and HadGEM2-ES), and two RCP emissions scenarios (RCP 2.6 and RCP 8.5). Additionally, we applied three statistical thresholds (derived from Maxent output) to the probability distribution maps output by Maxent to define areas of suitable habitat as presence/absence (1/0) binary maps: Liberal (Minimum Training Presence), Intermediate (Fixed 10 Cumulative), and Strict (Maximum Test Sensitivity plus Specificity). A gradient of thresholds reduces the influence of a single threshold on predictions of suitable habitat (Araujo and New 2007; Nenzen and Araujo 2011). Our ensemble design resulted in 27 model predictions per species.

We used the null models method developed by Raes and ter Steege (2007) to test the efficacy of our models to predict suitable habitat better than random. We modeled a random selection of points from our dataset to generate occurrence data for our null models. We selected randomly selected points from the same geographic area used to build models for that species. Null models consisted of 999 sets of points. Within the 999 sets, we used four different numbers of randomly selected points (23, 66, 175, and 372). We selected these point values because species with n values from 20 to 400 had the highest area under the curve (AUC) values and as a general rule, as n increases, AUC decreases (Raes and ter Steege 2007). We then took the 999 AUC values for each null model and calculated their 95% confidence interval and used these to determine significance of our species models. If species models fell above the 95% confidence interval with an n equal to or greater than our null models, we can determine they can predict suitable habitat better than random. We also used a regularization multiplier value of four in contrast to the default value

of one. Regularization in Maxent is an option designed to account for model overfitting, a common problem in presence-only modeling. Overfitting occurs when Maxent predicts the functional niche to be smaller than the realized niche of any species. When we ran SDMs with the default regularization multiplier value, current projections were significantly smaller than their current known distribution. We chose to use a value of four because it corrected model overfitting and is a supported value to correct this issue (Radosavljevic and Anderson 2014).

Each binary map was clipped to a genus-based dispersal limitation to ensure realistic analyses for change in suitable habitat. We created dispersal limitations by buffering current USGS county-based range maps of each species (Lannoo 2005) by a determined yearly dispersal distance multiplied by the number of years from 2015 to both 2050 (35) and 2070 (55). We created dispersal distances for a best-case scenario in which species could move without limitation from habitat resistance. We based our dispersal distances on a genus-specific ability for amphibians to traverse suitable habitat based on previous records of dispersal distances (reviewed in Smith and Green 2005). This ranged from 20 km/y (*Rana* and *Anaxyrus*), 1 km/y (*Ambystoma*, *Hemidactylium*, *Notophthalmus*, *Hyla*, *Acris*, *Pseudacris*, *Eurycea*, *Gyrinophilus*, *Desmognathus*), and 100 m/y (*Plethodon*). Although these distances were greater than reported in previous studies, we wanted to assess changes in suitable habitat with generous dispersal abilities to quantify changes from climate and land-use with minimal affect from dispersal limitation while creating informed predictions.

Quantifying predicted changes in species suitable climatic habitat.—

We quantified differences in suitable habitat from current to future projections by grid cell counts from the reclassified binary maps clipped by the dispersal limits. We also clipped current projections by both the 2050 and 2070 dispersal distances so differences between current and future projections would be standardized. We report changes in suitable habitat as percentage changes in relation to current projected habitat. To quantify percentage changes, we subtracted the number of presence raster cells for each threshold for future projections from the number of presence raster cells for the corresponding threshold for the current projections and then divided the result by the presence cells for the respective current projection.

Quantifying predicted changes in species suitable climatic and land-use habitat.—

We used USGS forecasted scenarios for land cover based on storylines B1 and A2 (low emissions and high emissions, respectively) from the USGS EROS project to examine

the impact of current and predicted future land-use changes on predicted suitable habitat of amphibians. We downloaded current land-use data (Landsat imagery from 2011; Homer et al. 2015) from the National Land Cover Database from the USGS Multi-Resolution Land Characteristics Consortium website (USGS. 2015. Multi-Resolution Land Characteristics Consortium. Available from <http://www.mrlc.gov/index.php> [Accessed 15 January 2015]) and we downloaded future projected land-use data from the USGS Earth Resources Observation and Science Center dataset (USGS. 2015. Landcover Modeling. Available from <https://landcover-modeling.cr.usgs.gov> [Accessed 15 January 2015]). Next, we classified each land-use projected scenario map (current, 2050 B1, 2050 A2, 2070 B1, and 2070 A2) from its initial classification down to six land cover classes: open water, developed, forest, agriculture, grassland, and wetlands. We used each scenario map of projections of reclassified land-use to determine suitable land-use habitat for each genus modeled in climate-only SDMs by identifying suitable land-use categories for each genus. We determined land-use suitability by identifying common land-use categories at occurrence data localities with support from literature searches. For example, salamanders in the genus *Plethodon* rely solely on cutaneous respiration and therefore typically inhabit areas with a high amount of canopy cover, so we deemed land-use cells other than forest unsuitable for this genus. Thus, we removed cells of suitable land-use for each species representing suitable land-use for genera from the scenario map of projections of reclassified land-use to create maps showing only unsuitable habitat cells for each genus. Next, for each decade (current, 2050, and 2070), we clipped predicted suitable habitat projection maps from the climate-only SDM output with the scenario map of projections of reclassified land-use representing unsuitable habitat for each genus to create a series of maps predicting the impact of both predicted global climate change and land-use change (herein climate + land-use maps).

For climate + land-use maps, we used years 2050 and 2070 for future land-use data because it represents the best replacement for an average of years provided by WorldClim for climate data. We scaled all land-use data up from 30 m² grids for current data and 250 m² grids for future data to better match the spatial resolution of our climate data of 0.00083 degree grids (about 1 km²). As a result, we also reclassified our land-use data into broader categories (as mentioned above) as to not misrepresent any grids with a more specific category. Although data from the USGS Multi-Resolution Land Characteristics Consortium is based on a previous assessment of climate by the IPCC, the relative trends in climate change scenarios for the fourth and fifth assessments were similar, but differed in their predicted

values (e.g., RCP 2.6 and B1 represent the same trend in emissions but with higher radiative forcing values in the fifth assessment scenarios). Land-use predictions based on the IPCC fourth assessment, therefore, are a conservative estimate compared to what may be projected according to the AR5 emissions: all have increased.

Quantifying predicted changes in species richness.—We developed species richness maps to quantify the changes in habitat suitability across all species from current projections to future scenarios in both climate-only and climate + land-use predictions. We created richness maps for each projected scenario by overlapping projections for each species within the same scenario. This assigned values to each grid cell with the number of species with a presence value in that cell. We present richness maps for our study averaged across decades (current, 2050, and 2070). We also used Level III Ecoregions of the U.S. Environmental Protection Agency (EPA) to assess species richness changes within our study area, which allowed us to identify areas of important climatic and land-use refuge. Each ecoregion received its respective weighted average of richness within its boundaries for each timeline. We did this to assign a richness value to each ecoregion to identify ecoregions that sustained a high amount of species richness from current to future projections.

Statistical analyses.—We used a two-way ANOVA to determine whether percentage changes in predicted suitable habitat or ecoregion species richness (dependent variables) differed between climate-only and climate + land-use maps and decade (2050 or 2070). Ensemble model designs inherently have multiple factors potentially influencing the dependent variable. We attempted to gain a better understanding of how our modeling factors may influence suitable habitat changes by using general linear models (GLMs) to examine whether GCM, emissions scenario, threshold, or latitude predicted the percentage changes in suitable habitat separately for each future decade. The interaction term between latitude and threshold for the GLM was significant; therefore, we used a one-way ANOVA to examine whether percentage change in suitable habitat differed across thresholds and we used Bonferroni correction to determine statistical significance. We calculated the centroid of each species range (Lannoo 2005) and we used the latitude coordinate from those centroids as a continuous predictor variable in the GLMs. This variable was important to include in the GLMs because there is a potential that species adapted to warmer climates (species with lower latitude centroids) may be affected differently than species adapted to cooler climates (species with higher latitude centroids). We

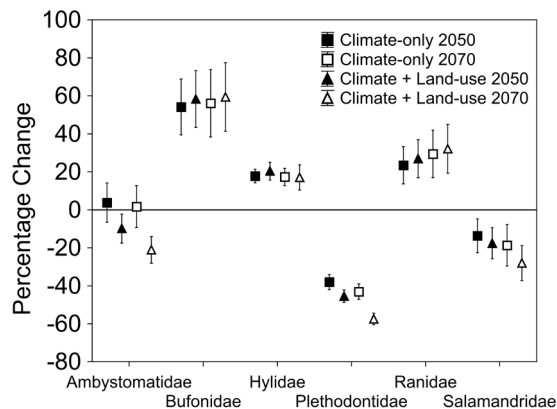


FIGURE 3. Mean (\pm SE) percentage change in predicted suitable habitat for amphibians from current to 2050 and 2070 projections for Climate-only and Climate + Land-use projections across families. Line at zero percent represents the cut-off for families that either gain (above line) or lose (below line) suitable habitat.

corrected our percentage changes for statistical analyses by adding a constant to each value to eliminate negative values. For each significant ANOVA, we used a Tukey HSD multiple comparisons test to find significant pairwise differences. We used STATISTICA 12.0 (Statsoft, Inc., Tulsa, OK) to analyze data with $\alpha = 0.05$.

RESULTS

Climate-only models predicted an average decline of suitable habitat for 21 of 33 species (63%) across all scenarios in 2050 and 22 of 33 species (66%) across all scenarios in 2070 (Appendix A). Average predicted losses in suitable habitat affected 14 (CCSM: RCP 2.6 for 2070) to 24 species (Hadley: RCP 8.5 for 2070) in modeled climate scenarios (Appendix A) where 12 of those species were predicted to lose, on average, > 90% of their current modeled suitable habitat. This scenario also predicted the highest increase in suitable habitat for any species with *Rana sphenocephala* projected to gain an average of 301% of its current predicted suitable habitat. Increases in suitable habitat were predicted for nine species in all model scenarios while 13 species were predicted to lose suitable habitat in all scenarios (Appendix A). All families experienced a species with predicted declines in suitable habitat; however, some

TABLE 1. Results from two-way ANOVA table investigating differences in percentage suitable habitat change for amphibians in Climate-only and Climate + land-use SDMs.

Effect	df	MS	F	P
SDM	1	18,385.2	2.608	0.106
Decade	1	4,121.5	0.584	0.444
SDM×Decade	1	2,520.0	0.357	0.549
Error	1,550	7,047.2		

families were predicted to lose a higher percentage of their current predicted suitable habitat than others.

Suitable habitat changes were not significantly different between climate-only models and the climate + land-use predictions across all species (Table 1; Fig. 3). For example, climate + land-use 2050 predictions resulted in 21 of 33 species predicted to lose suitable habitat in some capacity while seven of those species lost > 50% of their current predicted suitable habitat (Appendix B). Predictions for 2070 resulted in 25 of 33 species losing suitable habitat in some capacity and 11 of those species losing > 50% of suitable habitat (Appendix B). Additionally, climate + land-use results predicted 15 species to lose suitable habitat across all scenarios while six species gained suitable habitat across all scenarios. Amphibian families varied in their responses from predictions including land-use where Ambystomatidae, Plethodontidae, and Salamandridae experienced decreases in their average suitable habitat from climate-only to climate + land-use SDMs. Yet Bufonidae, Hylidae and Ranidae experienced a predicted increase in suitable habitat after land-use was included (Fig. 3).

Species richness was not significantly different across decades (Table 2), where mean species richness across the study region remained relatively constant from current predictions to predictions for 2050 and 2070 (Fig. 4). However, the highest richness values dropped from 28 species in current projections in areas to 23 species in 2050 and 22 species in 2070 projections (Fig. 4). Many ecoregions also experienced declines in richness losing an average of six or more species, while other ecoregions were predicted to increase in species richness, namely ecoregions toward the northern portions of the Midwest (Figs. 1 and 4), which is in contrast to our hypothesis that higher elevation areas would offer refuge compared to other areas. For example, the Lake Manitoba/Agassiz Plain, Northern Glaciated Plains, Northern Lakes and Forests, Northern Minnesota Wetlands, and North Central Hardwood Forests ecoregions were predicted to gain nearly two species from current to both 2050 and 2070 predictions (Figs. 4 and 5).

With respect to the ensemble model factors and biotic characteristics that predicted the percentage

TABLE 2. Results from two-way ANOVA table investigating differences in species richness of amphibians in Climate-only and Climate + land-use SDMs.

Effect	df	MS	F	P
SDM	1	43.63	2.564	0.109
Decade	1	17.95	1.055	0.304
SDM×Decade	1	0.850	0.050	0.822
Error	1,052	17.01		

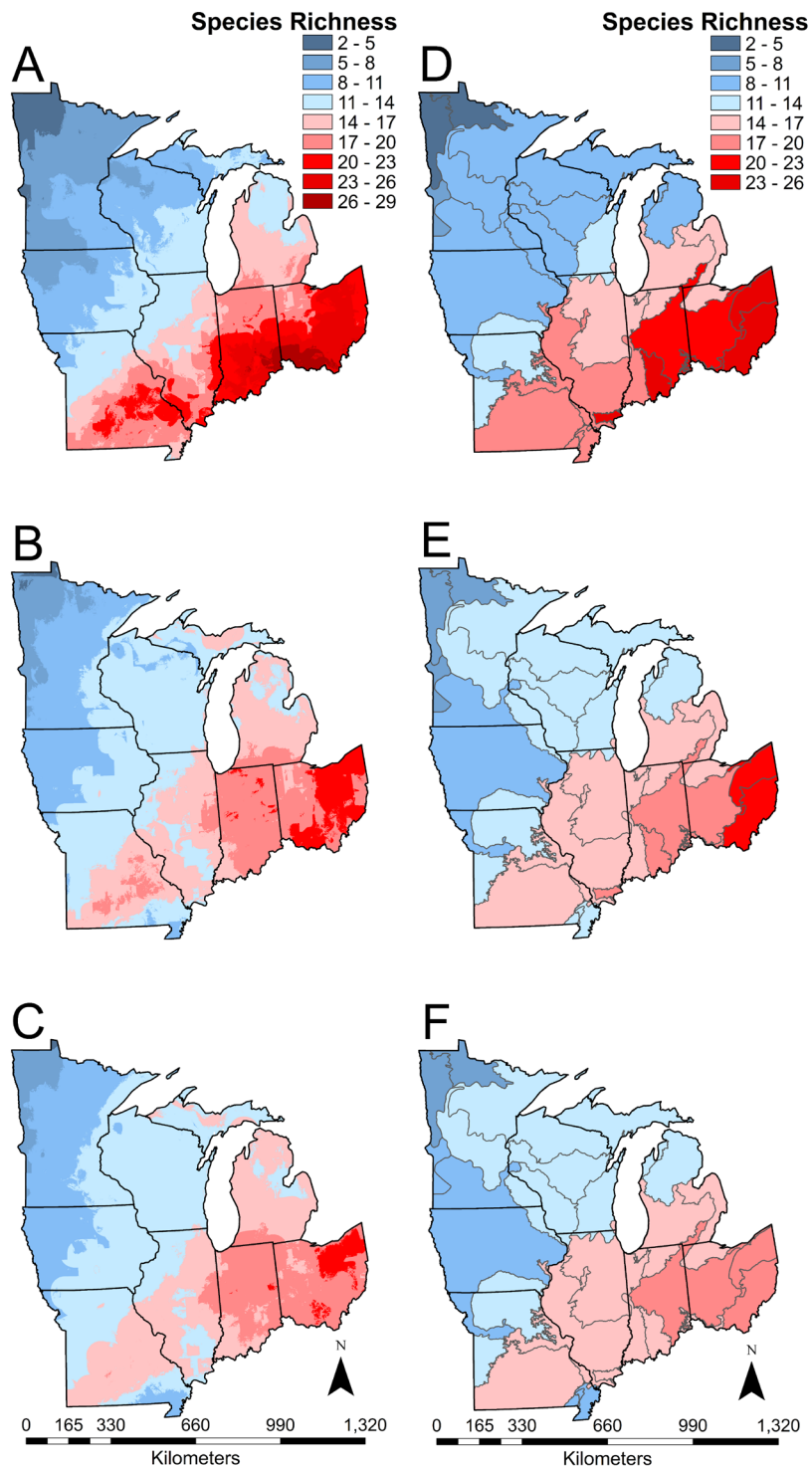


FIGURE 4. Species richness (weighted average of the number of species with suitable habitat) of amphibians for entire Midwestern region of the U.S. in Current (A), 2050 (B), and 2070 (C). Species richness for the U.S. Environmental Protection Agency (EPA) Level III Ecoregions in Current (D), 2050 (E), and 2070 (F). Red and light coloration indicates higher species richness and blue or dark coloration indicates lower species richness.

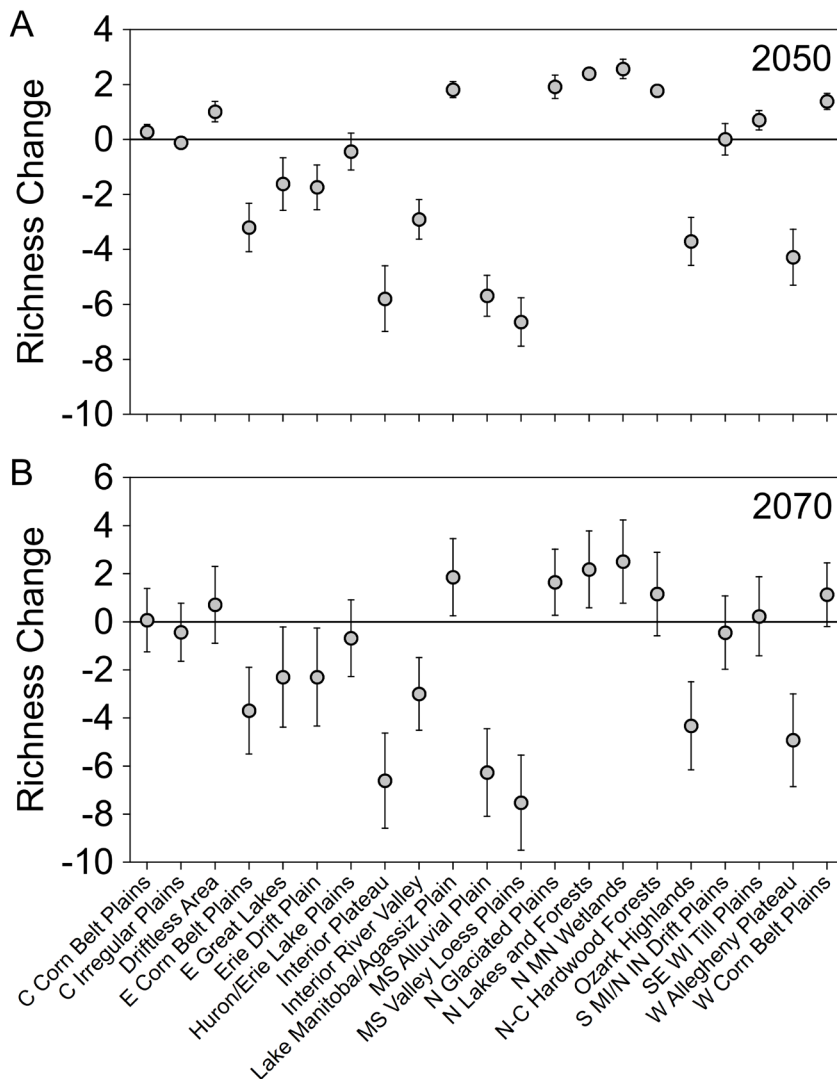


FIGURE 4. Mean (\pm SE) species richness change of amphibians (weighted average of the number of species with suitable habitat) within the U.S. Environmental Protection Agency (EPA) Level III Ecoregions across the Midwestern U.S. from Current to (A) 2050 and (B) 2070 projections.

changes in suitable habitat, model factors such as GCM and emissions scenario were not significant in their influence on percentage changes in predicted suitable habitat singly or in any interaction term (Table 3). As a result, for other analyses, we did not separate GCM or emissions scenario, instead we report results as averages across GCMs and emissions scenarios, separated only by each future decade (2050 and 2070). Both 2050 and 2070 projections had significant influence from latitude, threshold, and the interaction between the two on percentage changes in predicted suitable habitat (Table 3). Percentage change in suitable habitat did not vary significantly across thresholds for 2050 ($F_{2, 393} = 0.799, P = 0.450$) or 2070 ($F_{2, 393} = 0.873, P = 0.418$). Latitude had a significant negative relationship on percentage changes in predicted suitable habitat for all

three thresholds (Fig. 6) indicating species with current distributions in the southern portion of the Midwest were more likely to have a predicted increase in suitable habitat while species with current distributions in the northern portion were more likely to have predicted declines in suitable habitat in the study region. The strict threshold (Maximum Test Sensitivity plus Specificity) had the strongest negative relationship with latitude and percentage change in predicted suitable habitat while the liberal threshold (Minimum Training Presence) had the weakest relationship with latitude and percentage changes (Fig. 6). For families, all slopes were significant except for Plethodontidae (Table 4) while the strongest relationships existed for Bufonidae and Hylidae (Table 4). Bioclimatic variables with greatest contribution to models varied across family (Fig. 2). However, b1

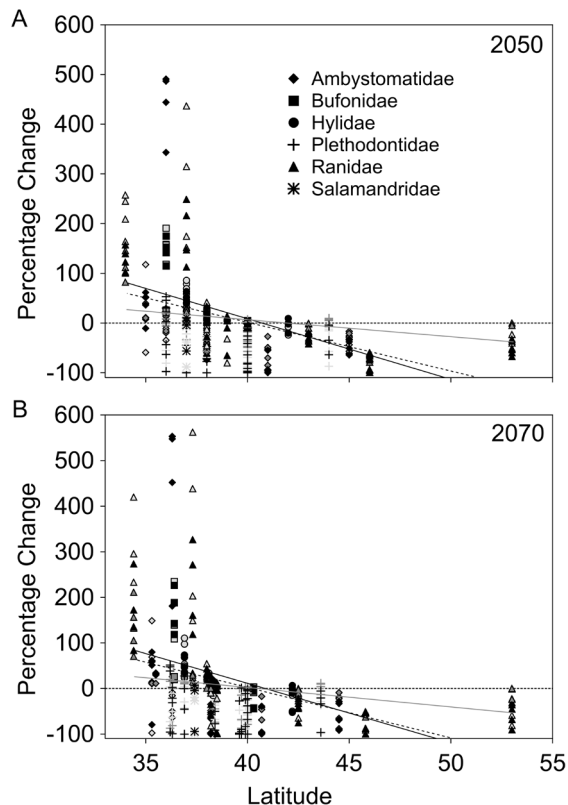


FIGURE 6. Relationship between latitude and percentage of suitable habitat change for amphibians from current suitable habitat to (A) 2050 and (B) 2070 projections for each family examined categorized by model threshold. Each point represents a threshold projection for each species, categorized by family: Intermediate threshold = light gray points, dashed black line; Liberal threshold = dark gray points, solid gray line; Strict threshold = black points, solid black line. Lines of fit represent significant effect of each threshold on percentage changes.

(Mean Annual Temperature) had the highest percentage of contribution to models for four of six families (Fig. 2).

Area under the curve values were on average 0.938 (± 0.037 SD) for all species modeled ranging from 0.852 to 0.996 (Appendix C). Null model AUC confidence limits ranged from 0.903 ($n = 23$) to 0.895 ($n = 372$). Only four species had AUC values less than our highest null model AUC (0.903, $n = 23$). However, these species had greater than 1,000 occurrence points used in models, greatly exceeding n values for our null models. Therefore, we determined our models were able to predict a species climatic niche better than random.

DISCUSSION

We predicted a large proportion of Midwestern amphibians to lose significant portions of their current suitable habitat under future climate change scenarios. Over 60% of the species modeled in both 2050 and

2070 projections lost predicted suitable habitat in some capacity, with many species predicted to lose all suitable habitat within the Midwest. As a result, species richness also declined from current to both 2050 and 2070 projections. Our results are consistent with other amphibian bioclimatic species distribution models that show significant declines in suitable habitat for amphibians in the United States (Milanovich et al. 2010; Barrett et al. 2014; Sutton et al. 2015) and with studies over larger geographic areas that predicted expansions in suitable habitat for a few species (Araujo et al. 2006; Lawler et al. 2010). We also predicted large northerly shifts in suitable habitat for many species as the southern limit of their current distributions shifted northward from current to future projections, also consistent with other studies. For example, Lawler et al. (2010) predicted a northerly shift in the suitable habitat of *Rana pipiens* across the western hemisphere, a shift our models also predicted, which resulted in significant losses of predicted suitable habitat for this species in the Midwest. Northward shifts of suitable habitat within the Midwest were visually noticeable in many future predictions and likely contributed to the predicted gain in species richness in northern portions of our study region and loss in richness in the southern portions. Contrary to our hypothesis, predicted land-use changes did not have a significant effect over predicted suitable habitat; thus, suggesting that predictions of global climate change may be the primary drivers of large-scale amphibian distribution changes in the Midwest.

A majority of amphibian SDM studies limit their focus specifically to climate without incorporating land-use, similar to our climate-only SDMs. However, there exists a large body of evidence that supports land-use and its role in amphibian habitat suitability (Price et al. 2011; Scheffers and Paszkowski 2012; Peterman and Semlitsch 2013; Osbourn et al. 2014). Although we hypothesized including land-use change into SDMs would have an increased negative effect on suitable habitat, our results indicate that there was no significant difference in changes in suitable habitat from current to future projections between climate-only and climate + land-use. Currently more than 50% of the Midwest is used for agriculture while only 25% is forested (Homer et al. 2015) and thus, the threshold at which land-use changes in our study region affect amphibians may have already been surpassed where changes in land-use may be minimal compared to the expansive changes in climate, showing little effect in our predictions. For example, a study by Rhemtulla et al. (2007) showed land cover changes in Wisconsin from 1850 to 1935 were significantly greater than subsequent changes from 1935 until 1993 where the nature of those changes consisted mostly of a loss in forest land cover and increases in cropland. As a result, future effects from

TABLE 3. Results from general linear model investigating the influence of model variables on percentage suitable habitat change for amphibians in 2050 and 2070 for Climate-only SDMs.

Effect	df	2050			2070		
		MS	F	P	MS	F	P
GCM	1	14.77	0.002	0.958	92.14	0.012	0.910
Emissions	1	3057.64	0.557	0.455	13911.74	1.909	0.167
Threshold	2	31493.78	5.745	0.003	38366.38	5.266	≤ 0.001
Latitude	1	333444.54	60.834	≤ 0.001	443281.88	60.849	≤ 0.001
GCM×Emissions	1	2756.68	0.502	0.478	14645.41	2.010	0.157
GCM×Threshold	2	2784.39	0.507	0.602	1268.22	0.174	0.840
Emissions×Threshold	2	660.29	0.120	0.886	1355.45	0.186	0.830
GCM×Latitude	1	165.83	0.030	0.862	824.23	0.113	0.736
Emissions×Latitude	1	3809.96	0.695	0.404	17934.55	2.461	0.117
Threshold×Latitude	2	29959.79	5.465	0.004	35842.93	4.920	0.007
Error	381	5481.15			7284.90		

climate change may overshadow the effects that land-use changes may have on suitable habitat. Additionally, we predicted 100% current suitable habitat loss in many species for some scenarios in climate-only SDMs, which provided no opportunity for land-use to affect predictions in suitable habitat. While considering these factors, we did observe variation in suitable habitat between climate-only and climate + land-use SDMs across families where we predicted a decrease in suitable

habitat when land-use is considered for some families (Ambystomatidae, Plethodontidae, and Salamandridae) and an increase in suitable habitat for others (Bufonidae, Hylidae, and Ranidae). Interestingly, this also seems to be partitioned based on taxonomic order where anurans (frogs and toads) gained suitable habitat while urodeles (salamanders) lost suitable habitat with the inclusion of land-use. This is likely an artifact of the general land-use tolerance of Bufonidae, Hylidae and Ranidae species

TABLE 4. Linear fit data for the relationships between percentage changes (PC) and latitude (L) for each threshold and for each amphibian family. Data are separated by decade. Abbreviations are n = number of species for each family, MTP = Minimum Training Presence threshold (Liberal), F10 = Fixed 10 Cumulative threshold (Intermediate), MTSPS = Maximum Test Sensitivity plus Specificity threshold (Strict).

Family	n	Threshold	2050			2070		
			Linear fit equation	r ²	P	Linear fit equation	r ²	P
Ambystomatidae	8	F10	PC = 308.48-8.42×L	0.300	≤ 0.001	PC = 381.09-10.39×L	0.259	0.003
		MTP	PC = 200.42-5.56×L	0.337	≤ 0.001	PC = 270.90-7.46×L	0.321	≤ 0.001
		MTSPS	PC = 948.48-23.69×L	0.203	0.009	PC = 983.76-24.64×L	0.177	0.016
Bufonidae	2	F10	PC = 1572.32-39.35×L	0.946	≤ 0.001	PC = 1822.07-45.44×L	0.854	≤ 0.001
		MTP	PC = 249.69-6.25×L	0.986	≤ 0.001	PC = 274.31-6.86×L	0.941	≤ 0.001
		MTSPS	PC = 1467.53-36.70×L	0.955	≤ 0.001	PC = 1869.23-46.71×L	0.890	≤ 0.001
Hylidae	4	F10	PC = 515.56-12.67×L	0.592	≤ 0.001	PC = 624.65-15.47×L	0.569	≤ 0.001
		MTP	PC = 178.44-4.36×L	0.269	0.039	PC = 200.03-4.89×L	0.304	0.026
		MTSPS	PC = 343.60-8.35×L	0.578	≤ 0.001	PC = 462.09-11.39×L	0.605	≤ 0.001
Plethodontidae	10	F10	PC = 51.36-2.69×L	0.025	0.328	PC = 75.15-3.30×L	0.032	0.268
		MTP	PC = -35.44+0.49×L	0.001	0.828	PC = -98.90+1.82×L	0.008	0.582
		MTSPS	PC = 111.90-3.97×L	0.038	0.222	PC = 139.51-4.79×L	0.045	0.185
Ranidae	8	F10	PC = 595.78-13.50×L	0.355	≤ 0.001	PC = 715.13-16.16×L	0.293	0.268
		MTP	PC = 209.55-4.87×L	0.353	≤ 0.001	PC = 251.63-5.89×L	0.313	≤ 0.001
		MTSPS	PC = 460.43-10.77×L	0.475	≤ 0.001	PC = 538.72-12.53×L	0.045	0.185
Total	33	F10	PC = 361.75-9.31×L	0.1588	≤ 0.001	PC = 431.48-11.03×L	0.1410	≤ 0.001
		MTP	PC = 133.57-3.51×L	0.1355	≤ 0.001	PC = 155.87-4.17×L	0.1069	≤ 0.001
		MTSPS	PC = 470.63-11.82×L	0.1805	≤ 0.001	PC = 516.69-12.98×L	0.1673	≤ 0.001

as well as the relative land-use specificity of species in the salamander families predicted to decline. Species with the ability to persist and survive in relatively degraded habitat (e.g., agricultural or urban areas) may not be as negatively impacted by future changes. Land-use, although not significantly affecting changes in suitable habitat in our study, may have a significant impact on dispersal abilities of amphibians in the future as traversing unfavorable habitat is a source of high mortality for amphibians (Lehtinen et al. 1999; Stevens et al. 2004; Goldberg and Waits 2010). Yet, we should still be cautious considering our predictions for dispersal as many studies have suggested mobility of amphibians will decrease during episodes of unfavorable climate (Rohr and Palmer 2013).

Changes in predicted suitable habitat were largely driven by the current climatic adaptation (e.g., latitude) of each species. Therefore, species with southerly current distributions were more likely to gain predicted suitable habitat within the Midwest while the reverse was predicted for northerly distributed species. Yet, this relationship was not significant for Plethodontidae, which experienced widespread declines in suitable habitat for species with current known distributions from southern to northern portions of the Midwest. However, Plethodontidae are closely associated with specific microclimates (Peterman and Semlitsch 2013) and may have a more restrictive climatic niche. This along with their low dispersal distances may have potentially lead to their predicted declines across the latitude gradient. For other families, latitude was a significant driver, likely an effect of the shift in climate regimes in future decades (Feng et al. 2014). However, our data are limited in what we can predict about the effects of each species distribution outside of the Midwest, therefore we cannot confidently conclude the degree to which a species distribution changed outside of our study region from our current analyses. Predicted declines within our study area do not translate to overall declines in suitable habitat across a total species distribution. The complete loss of species within our study region represents a high degree of species turnover within the Midwest, with some ecoregions losing on average six or more species. In some instances, shifts were significant and occurred over several kilometers. For example, *R. sphenoccephala* expanded the northern limit of its predicted distribution from northern Missouri to southern Minnesota, a shift of more than 400 km by 2070. Yet *R. septentrionalis* and *R. pipiens*, species within the same genus with current distributions centered further north, lost their entire predicted suitable habitat in the Midwest in many scenarios. As a result, we predicted that species richness in the northern portions of our study region would increase, while we predicted that species richness in the southern portions would decrease. This illustrates that

some southern distributed species lost suitable habitat in the southern portion of the study region. However, richness in the southern portion of the Midwest may increase as species to the south move into the study region, if they follow similar trends to species in which we modeled in our study.

We investigated the potential influence of modeling factors on changes in predicted suitable habitat to identify important drivers of changes. Climate scenarios (e.g., GCM or RCP) did not significantly influence changes in predicted suitable habitat for amphibians likely because of their relatively close agreement in greenhouse gas emissions up to 2050 (van Vuuren et al. 2011) and the potentially low threshold of climate change at which amphibians are affected. However, the interaction of threshold and latitude significantly influenced predicted suitable habitat changes. Others have noted caution in regard to using Maxent's threshold values because they are unrelated to any biological or ecological estimate, making their predictions somewhat arbitrary (Merow et al. 2013) and may also be affected by size of study area (Nenzen and Araujo 2011). This supports growing evidence towards the importance of using a multi-threshold approach. Further, we underscore the importance of threshold choice in model predictions, as our results indicate their significant interaction with latitude on model predictions.

Ecological niche models are limited in their capacity to predict the realized niche of any given species as there are a variety of both biotic and abiotic variables that influence suitable amphibian habitat (e.g., competition, predation, chemical pollution, and disease). The inherent variability and multifaceted nature of these variables make them difficult to include in predictive models, especially doing so across our large study region (Holt 2009; Kissling et al. 2012). Although we did not build a complete ecological niche for Midwest amphibians, the relationships we modeled between climate and land-use are important to understand how climate and land-use influence habitat for amphibians, two major drivers of amphibian habitat suitability. With these baseline relationships, we can then include more complex relationships in the future. Occurrence-only SDMs are also limited given that occurrence data originate from multiple sources with varying sampling efforts and techniques. Such variation has the potential to create biases between data from one source to another (Ruiz-Gutierrez and Zipkin 2011) leading to skewed representation of environmental variables in heavily sampled locations. We addressed this bias with two techniques agreed as effective solutions (Barrett et al. 2014; Fourcade et al. 2014), yet it is difficult to identify if these techniques correct this issue fully. Therefore, we are limited in how we interpret our results. Our SDMs should not be seen as specific forecasts but

as a tool to gauge the severity and broad patterns of future changes. For example, we predicted northward expansions of suitable habitat for several species. Although each species may not realize this expansion in the future, the overall trend of northward expansions in the Midwest is meaningful. Understanding these spatial and temporal trends may provide important information for future conservation efforts, especially for local and state agencies that manage lands at the edges of species distributions. From these data we can gauge which species are most at-risk within the Midwest and identify areas in which conservation efforts may be most fruitful.

We suggest species of greatest conservation priority within the Midwest to be species that experienced a loss in suitable habitat on average > 50% of their current predicted suitable habitat. Predictions for 2050 identify five species with highest conservation priority: *Ambystoma jeffersonianum*, *Eurycea longicauda*, *Gyrinophilus porphyriticus*, *Rana septentrionalis*, and *Plethodon electromorphus*. Predictions for 2070 identify seven species with highest conservation priority: *Ambystoma barbouri*, *Ambystoma jeffersonianum*, *Ambystoma laterale*, *Eurycea longicauda*, *Gyrinophilus porphyriticus*, *Rana septentrionalis*, *Plethodon electromorphus*. Although we did not quantify changes in suitable habitat across the entire species distribution, we do quantify significant losses in the Midwest. Therefore, conservation efforts focused specifically on conserving species richness and diversity at a local or regional scale should prioritize these species. In addition, local agencies may need to consider enhanced conservation efforts for any species in which their land encompasses the edge of their distribution.

Including land-use into model predictions did not have a significant effect on changes in suitable habitat; however, our study may be limited to determine the overall effect land-use changes have on amphibians. For example, the scale at which we investigated land-use (1 km²) and the broader land-use categories we used to define suitable and unsuitable habitat for amphibians likely loses a great deal of variation in specific habitat characteristics that define suitable habitat for amphibians. This may result in areas that we define as suitable which may be unsuitable at a finer spatial scale (< 1 km²). However, finer resolution data (30 m²), although available, does not represent the fine-scale habitat characteristics in which amphibians use (< 1 m²). Our data represent a broader classification at a regional scale, and thus, should be interpreted as the relationship between amphibians and their association with broad patterns of climate changes and changes in land-use. We feel these broad associations to be meaningful in the context of landscape conservation. Additionally, our data do not represent the notion that land-use is an unimportant factor in determining suitable habitat for

amphibians. Rather, our data underscore the drastic effects of climate change relative to land-use changes and therein the importance for addressing climate change in landscape conservation for amphibians in the Midwest.

The ecological niche used to predict suitable habitat for SDMs is derived from climate variables for several known habitat localities. However, it is not known if the climate at the collection of localities represents the total variation that a species can tolerate. Understanding the climatic variation that a species can tolerate is important because climate change will not consistently shift from year to year, but will likely have inter- and intra-annual variation significantly impacting the ability for species to survive (Early and Sax 2011). In addition, it is possible that species will adapt to novel climates over time, increasing their physiological tolerances. However, the plasticity of most species is unknown. A mechanistic and correlative approach could be used to test the physiological limits of species and transfer that knowledge to the predicted spatial distribution of climate. Mechanistic models have been used to accurately project amphibian distributions (Kearney et al. 2008) and will provide a more comprehensive prediction of the climatic niche of a given species (Kearney et al. 2010). However, we lack the data on the physiological limits of most species; therefore, there is a need for more mechanistic investigations at the species level. Such investigations will help build more robust models and better-inform climate-based predictions of habitat changes.

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APPENDIX A. Percentage changes from current to the ensemble of projections for each species in 2050 and 2070 for climate-only models of amphibian species.

Species	2050					2070			
	CCSM 2.6	CCSM 8.5	Hadley 2.6	Hadley 8.5		CCSM 2.6	CCSM 8.5	Hadley 2.6	Hadley 8.5
<i>Ambystoma annulatum</i>	166.77	163.88	142.21	97.28	156.35	182.88	184.89	22.26	166.77
<i>Anaxyrus americanus</i>	2.91	3.14	-1.43	-7.46	0.22	0.73	-2.03	-31.98	2.91
<i>Ambystoma barbouri</i>	-29.88	-49.16	-56.30	-57.48	-7.47	-59.22	-48.62	-100.00	-29.88
<i>Acris crepitans</i>	41.08	57.23	49.19	65.22	37.74	71.85	48.96	77.88	41.08
<i>Anaxyrus fowleri</i>	84.94	112.47	108.01	130.64	82.50	134.24	102.58	162.52	84.94
<i>Ambystoma jeffersonianum</i>	-44.96	-79.24	-92.66	-90.18	-32.81	-88.59	-79.50	-100.00	-44.96
<i>Ambystoma laterale</i>	-25.84	-42.61	-29.39	-60.98	-18.99	-67.71	-28.26	-90.05	-25.84
<i>Ambystoma maculatum</i>	6.73	8.41	-9.58	-45.33	9.97	6.93	0.42	-64.73	6.73
<i>Ambystoma opacum</i>	31.49	62.92	34.10	-20.11	43.41	80.76	43.80	-55.43	31.49
<i>Ambystoma tigrinum</i>	12.69	16.44	12.83	15.25	12.61	18.33	16.78	15.47	12.69
<i>Ambystoma texanum</i>	20.87	21.13	20.86	21.10	24.01	25.20	25.28	25.27	20.87
<i>Desmognathus fuscus</i>	-7.81	-18.19	-37.52	-84.82	-10.11	-29.57	-39.85	-100.00	-7.81
<i>Eurycea bislineata/ Eurycea cirrigera</i>	-14.25	0.12	-44.77	-82.71	-4.75	-20.21	-57.70	-99.82	-14.25
<i>Eurycea longicauda</i>	-37.76	-61.62	-41.93	-75.74	-35.49	-77.72	-52.60	-100.00	-37.76
<i>Eurycea lucifuga</i>	14.18	-33.43	-38.29	-99.70	15.22	-39.63	9.00	-100.00	14.18
<i>Gyrinophilus porphyriticus</i>	-56.03	-62.05	-66.67	-85.67	-24.76	-65.85	-66.45	-100.00	-56.03
<i>Hyla versicolor/ Hyla chrysoscelis</i>	12.85	17.26	14.25	19.13	10.44	20.95	16.24	18.17	12.85
<i>Hemidactylium scutatum</i>	-4.73	-16.15	-54.55	-78.84	-2.61	-36.72	-45.96	-92.87	-4.73
<i>Notophthalmus viridescens</i>	6.83	-0.24	-13.56	-47.66	5.45	-7.22	-9.37	-63.64	6.83
<i>Pseudacris crucifer</i>	8.44	7.99	8.73	1.68	5.61	7.31	10.99	-6.04	8.44
<i>Plethodon dorsalis</i>	13.78	25.24	22.40	11.15	19.12	23.49	24.85	-85.13	13.78
<i>Plethodon electromorphus</i>	-14.45	-44.91	-96.92	-100.00	-8.84	-89.72	-75.94	-100.00	-14.45
<i>Plethodon cinereus/ Plethodon serratus</i>	-2.92	-5.37	-27.26	-48.52	0.00	-20.16	-12.59	-69.24	-2.92
<i>Plethodon albagula/ Plethodon glutinosus</i>	-0.14	-33.13	-49.97	-79.86	-2.79	-27.97	-27.24	-93.45	-0.14
<i>Pseudacris triseriata</i>	2.72	-3.05	-3.19	-14.79	1.54	-8.29	-2.48	-34.29	2.72
<i>Rana blairi</i>	95.86	186.79	116.63	235.99	97.12	247.59	130.95	301.09	95.86
<i>Rana catesbeiana</i>	18.06	18.73	14.91	25.12	13.87	25.72	19.51	32.71	18.06
<i>Rana clamitans</i>	3.30	0.62	-2.69	-23.36	4.97	1.27	2.77	-38.77	3.30
<i>Rana palustris</i>	11.61	5.14	-10.54	-44.89	8.58	1.25	-4.76	-61.97	11.61
<i>Rana pipiens</i>	-12.88	-22.14	-13.52	-29.65	-12.24	-31.79	-20.69	-55.68	-12.88
<i>Rana septentrionalis</i>	-63.18	-87.02	-68.94	-92.65	-52.48	-96.71	-79.32	-100.00	-63.18
<i>Rana sphenocephala</i>	115.43	165.32	144.66	186.61	95.30	207.96	157.78	301.25	115.43
<i>Rana sylvatica</i>	-19.99	-31.27	-30.85	-41.27	-19.53	-42.74	-25.75	-65.13	-19.99

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APPENDIX B. Percentage changes from current to the ensemble of projections for each species in 2050 and 2070 for climate + land-use models of amphibians.

Species	2050				2070				
	CCSM 2.6	CCSM 8.5	Hadley 2.6	Hadley 8.5	CCSM 2.6	CCSM 8.5	Hadley 2.6	Hadley 8.5	
<i>Ambystoma annulatum</i>	91.99	106.91	73.69	49.08	53.44	95.69	57.45	-29.05	91.99
<i>Anaxyrus americanus</i>	5.52	7.42	0.94	-3.38	1.57	4.48	-0.62	-28.88	5.52
<i>Ambystoma barbouri</i>	-55.51	-75.82	-82.88	-79.77	-49.42	-86.55	-69.46	-100.00	-55.51
<i>Acris crepitans</i>	25.43	81.61	42.84	102.72	5.08	116.54	25.75	133.88	25.43
<i>Anaxyrus fowleri</i>	87.60	118.91	111.52	138.28	82.72	141.20	103.27	171.39	87.60
<i>Ambystoma jeffersonianum</i>	-62.13	-80.86	-93.74	-94.45	-63.01	-92.14	-89.12	-100.00	-62.13
<i>Ambystoma laterale</i>	-18.70	-21.08	-21.09	-39.87	-20.57	-43.88	-23.69	-81.14	-18.70
<i>Ambystoma maculatum</i>	-3.28	13.81	-21.03	-48.37	-10.99	9.44	-17.33	-63.17	-3.28
<i>Ambystoma opacum</i>	0.14	38.60	10.45	-24.33	-8.87	45.72	-8.63	-61.45	0.14
<i>Ambystoma tigrinum</i>	15.60	41.17	14.90	40.00	3.57	42.61	14.91	38.99	15.60
<i>Ambystoma texanum</i>	-3.49	9.61	-3.91	9.39	-16.14	6.59	-15.61	6.30	-3.49
<i>Desmognathus fuscus</i>	-23.22	-17.92	-43.97	-82.22	-37.65	-32.75	-55.97	-100.00	-23.22
<i>Eurycea bislineata/ E. cirrigera</i>	-34.16	-12.34	-46.56	-81.24	-43.72	-22.90	-75.38	-99.48	-34.16
<i>Eurycea longicauda</i>	-37.84	-66.14	-51.95	-76.50	-47.54	-86.62	-70.61	-100.00	-37.84
<i>Eurycea lucifuga</i>	-6.00	-44.54	-51.58	-99.52	-19.70	-64.99	-34.29	-100.00	-6.00
<i>Gyrinophilus porphyriticus</i>	-60.86	-62.71	-71.73	-82.17	-43.81	-67.19	-76.17	-100.00	-60.86
<i>Hyla versicolor/ H. chrysoscelis</i>	4.02	25.13	6.51	29.37	-9.29	30.09	-0.83	27.70	4.02
<i>Hemidactylium scutatum</i>	-18.81	-15.03	-59.80	-78.00	-27.20	-38.66	-56.57	-89.08	-18.81
<i>Notophthalmus viridescens</i>	-4.42	2.57	-21.84	-46.67	-15.56	-7.38	-26.85	-62.39	-4.42
<i>Pseudacris crucifer</i>	-1.04	10.40	-1.24	1.96	-12.94	10.25	-9.15	-4.22	-1.04
<i>Plethodon dorsalis</i>	-21.97	-2.28	-19.51	-11.54	-33.70	-8.77	-32.69	-94.31	-21.97
<i>Plethodon electromorphus</i>	-29.92	-47.99	-97.16	-100.00	-39.34	-92.00	-78.46	-100.00	-29.92
<i>Plethodon cinereus/ P. serratus</i>	-10.31	3.37	-26.49	-47.77	-19.36	-11.89	-25.86	-62.77	-10.31
<i>Plethodon albagula/ P. glutinosus</i>	-16.43	-34.23	-55.02	-76.80	-32.19	-35.23	-48.86	-93.49	-16.43
<i>Pseudacris triseriata</i>	0.46	6.33	-5.80	-3.01	-10.00	1.10	-11.75	-19.42	0.46
<i>Rana blairi</i>	102.50	196.27	123.02	246.72	101.86	257.83	135.70	313.52	102.50
<i>Rana catesbeiana</i>	21.94	24.41	18.61	31.39	16.16	31.55	22.05	39.18	21.94
<i>Rana clamitans</i>	6.00	4.86	-0.44	-20.72	6.39	5.12	3.99	-36.14	6.00
<i>Rana palustris</i>	14.47	9.49	-8.06	-42.28	9.92	4.70	-3.66	-60.36	14.47
<i>Rana pipiens</i>	-11.02	-18.96	-11.55	-26.33	-11.32	-28.95	-19.70	-53.39	-11.02
<i>Rana septentrionalis</i>	-63.26	-86.48	-68.98	-92.29	-52.48	-96.56	-79.24	-100.00	-63.26
<i>Rana sphenoccephala</i>	117.52	169.54	147.62	192.38	95.23	211.74	155.96	308.51	117.52
<i>Rana sylvatica</i>	-18.80	-29.00	-29.72	-38.86	-19.33	-40.98	-25.56	-63.37	-18.80

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APPENDIX C. The average AUC values for model runs which includes the values for the 33 study species of amphibians and four null models. Values are organized by AUC from highest to lowest. Null model values represent the 95% confidence limit for the 999 replicates.

Species	n	AUC
<i>Ambystoma annulatum</i>	21	0.996
<i>Ambystoma barbouri</i>	30	0.995
<i>Plethodon electromorphus</i>	70	0.991
<i>Eurycea lucifuga</i>	86	0.986
<i>Plethodon dorsalis</i>	55	0.983
<i>Eurycea longicauda</i>	114	0.980
<i>Ambystoma jeffersonianum</i>	144	0.980
<i>Rana septentrionalis</i>	140	0.967
<i>Ambystoma laterale</i>	103	0.965
<i>Hemidactylium scutatum</i>	293	0.961
<i>Ambystoma texanum</i>	335	0.958
<i>Rana blairi</i>	530	0.955
<i>Gyrinophilus porphyriticus</i>	743	0.953
<i>Plethodon slimy cmplx</i>	494	0.949
<i>Ambystoma opacum</i>	598	0.947
<i>Eurycea cirrigera</i>	614	0.946
<i>Ambystoma tigrinum</i>	203	0.943
<i>Plethodon redback cmplx</i>	676	0.941
<i>Desmognathus fuscus</i>	885	0.941
<i>Rana palustris</i>	797	0.933
<i>Ambystoma maculatum</i>	895	0.925
<i>Rana sphenoccephala</i>	1269	0.918
<i>Pseudacris crucifer</i>	704	0.914
<i>Pseudacris triseriata</i>	262	0.912
<i>Rana clamitans</i>	931	0.907
<i>Hyla gray cmplx</i>	745	0.906
<i>Acris crepitans</i>	980	0.906
<i>Anaxyrus woodhousii</i>	777	0.905
Null	175	0.904
<i>Rana pipiens</i>	486	0.904
Null	23	0.903
Null	66	0.902
<i>Anaxyrus americanus</i>	995	0.897
Null	371	0.896
<i>Notophthalmus viridescens</i>	1572	0.896
<i>Rana sylvatica</i>	1091	0.864
<i>Rana catesbeiana</i>	1660	0.852