


Climate change and range restriction of common salamanders in eastern Canada and the United States

Brian W. Widmer  | Thomas M. Gehring |
Benjamin W. Heumann | Kirsten E. Nicholson

Central Michigan University, Mount Pleasant,
MI 48858, USA

Correspondence

Brian W. Widmer, University of Missouri,
Columbia, MO 65211, USA.
Email: brianwidmer@missouri.edu

Present address

Brian W. Widmer, University of Missouri,
Columbia, MO 65203, USA.

Funding information

Central Michigan University (Department of
Biology, College of Science and Engineering,
Office of Research and Graduate Studies).

Abstract

The sensitivity of amphibian species to shifts in environmental conditions has been exhibited through long-term population studies and the projection of ecological niche models under expected conditions. Species in biodiversity hotspots have been the focus of ample predictive modeling studies, while, despite their significant ecological value, wide-ranging and common taxa have received less attention. We focused on predicting range restriction of the spotted salamander (*Ambystoma maculatum*), blue-spotted salamander (*A. laterale*), four-toed salamander (*Hemidactylium scutatum*), and red-backed salamander (*Plethodon cinereus*) under future climate scenarios. Using bias-corrected future climate data and biodiversity database records, we developed maximum entropy (MaxEnt) models under current conditions and for climate change projections in 2050 and 2070. We calculated positivity rates of species localities to represent proportions of habitat expected to remain climatically suitable with continued climate change. Models projected under future conditions predicted average positivity rates of 91% (89–93%) for the blue-spotted salamander, 23% (2–41%) for the spotted salamander, 4% (0.7–9%) for the four-toed salamander, and 61% (42–76%) for the red-backed salamander. Range restriction increased with time and greenhouse gas concentration for the spotted salamander, four-toed salamander, and red-backed

salamander. Common, widespread taxa that often receive less conservation resources than other species are at risk of experiencing significant losses to their climatic ranges as climate change continues. Efforts to maintain populations of species should be focused on regions expected to experience fewer climatic shifts such as the interior and northern zones of species' distributions.

KEYWORDS

blue-spotted salamander, climate change, climatic niche modeling, common species, four-toed salamander, MaxEnt, red-backed salamander, spotted-salamander

Amphibians are among the most threatened taxonomic groups amidst the Anthropocene mass extinction event (Hoffmann et al. 2010). The effects of changing climatic conditions from increased atmospheric greenhouse gas concentrations on ectothermic species compound with impacts of habitat loss and fragmentation resulting in exacerbated declines (Peterson et al. 2018). As climate change is predicted to increase in intensity with time, so is the physiological stress of thermal-sensitive species in regions with increasingly variable climate patterns (Pechl et al. 2017). Human-induced climatic perturbation and the resulting variations in temperature and precipitation patterns have affected and will continue to affect the ability of many sensitive species to persist in their native ranges (Brown et al. 2016). With the advent of species distribution models and ecological niche modeling, researchers have been able to make predictions as to how changing conditions, often in the context of climate change, may affect at-risk species in the future (Walls et al. 2013). While a plethora of studies have used modeling methods to predict declines of species in biodiversity hotspots (Malcolm et al. 2006, Fitzpatrick et al. 2008, Esser et al. 2019), there is potentially more value in assessing the vulnerability of widely distributed, common species to climate change because abundance of common species, not species richness, drives ecosystem service delivery and common species often decline rapidly in response to changing environmental conditions (Lindenmayer et al. 2011, Winfree et al. 2015). Additionally, species that are relatively common and exhibit wide geographic ranges are seldom considered at-risk or high priority compared to rare or geographically limited taxa (Gaston 2010). By building niche models using adequate data and the best-practice procedures, regions predicted to remain or become suitable (i.e., refugia) can be identified and used in management projects (La Marca et al. 2019).

Amphibians make suitable model organisms for climatic niche modeling because species are ectotherms and exhibit spatial patterns that are highly correlated with climatic variables (Wake and Vredenburg 2008, Pineda and Lobo 2009). Sutton et al. (2015) modeled areas of climate refugia under continued climate change for 28 salamander species in the northeastern United States and predicted mean refugia losses of 62% for plethodontid and 46% for ambystomatid species. Similarly, Milanovich et al. (2010) predicted climatic niche response of 41 plethodontid salamander species of the Appalachian Highlands and reported niche reductions of $\geq 20\%$ species at lower latitudes. Struecker and Milanovich (2017) modeled the responses of 33 salamander species across the midwestern United States to climate change and reported suitable habitat declines of 63% for 21 species in models projected to 2050 and 66% for 22 species in 2070-projected models. While studies using many species to predict climate change impacts are valuable for recognizing general threats to entire groups of organisms (e.g., salamanders) or to high diversity regions, focusing on a smaller number of species that share desired habitat characteristics can produce results with more specific applications (Flesch 2019, Lehtomäki et al. 2019).

We used similar techniques to assess the climatic niche vulnerabilities of 4 of the most common and wide-ranging salamander species of the eastern United States and Canada: spotted salamander (*Ambystoma*

maculatum), blue-spotted salamander (*A. laterale*), four-toed salamander (*Hemidactylium scutatum*), and red-backed salamander (*Plethodon cinereus*). We selected these species for their wide distributions, relative commonality, and importance in local food webs, biomass pyramids, and energy dynamics (Davic and Welsh 2004). The red-backed salamander is one of the most abundant vertebrates in northeastern North America and plays an important role in the regulation of invertebrate communities as a top-down predator (Walton et al. 2006). While the four-toed salamander exhibits a patchier distribution compared to the red-backed salamander, no plethodontid species ranges across a broader geographic extent (Herman and Bouzat 2016). Red-backed and four-toed salamanders are small, lungless species from the family Plethodontidae that breed terrestrially during warmer months of the year (Harris and Ludwig 2004, Cabe et al. 2007). While the eggs of the red-backed salamander are laid on land and develop directly to juveniles, four-toed salamander eggs are laid along the edges of aquatic areas (e.g., ponds) where hatched larvae move into to complete development before dispersing as juveniles (Banning et al. 2008). Of the 32 extant, relatively large-bodied terrestrial salamander species in the family Ambystomatidae, the blue-spotted salamander and spotted salamander exhibit 2 of the broadest geographic ranges with the latter found farther south from Texas to South Carolina, USA (Petranka 1998). Through depositing egg masses in ponds following late winter breeding events when ponds are still covered in ice, the blue-spotted salamander and spotted salamander facilitate the transfer of nutrients and energy between terrestrial and aquatic systems and support several trophic-level interactions (Regester et al. 2006, Thackeray et al. 2010, Earl et al. 2011). Additionally, these common salamanders are regarded as indicators of ecosystem health in assessments of sustainability of logging techniques (Pearce and Venier 2009). Their behavior and ecology are representative of many other species within their genera where geographic ranges and ecological preferences overlap.

Our objective was to model species climatic ranges, which can be defined as regions predicted to feature favorable conditions of the climatic variables used in model development. We quantified the proportions of current ranges that will feature unfavorable climatic conditions and thus restrict species persistence. Our hypotheses for model results were climatic range restriction will increase with time and atmospheric emission concentration, reductions in climatic suitability will be concentrated near the periphery of species' native ranges, and species with the broadest geographic extents (four-toed salamander and spotted salamander) will experience greater reductions in climatic range than species with more limited extents (red-backed salamander and blue-spotted salamander).

STUDY AREA

Our study area included a 4,801,993-km² section of the eastern United States and Canada, extending roughly from 29.6° to 56.2°N and -57.1° to -96.5°W. We defined our study area as the cumulative extent of environmental raster files used in species models. Overall, the study area is diverse in terms of physical geography. Biomes include temperate coniferous forests, temperate mixed forest, boreal forest, and temperate grasslands with urban and agriculture land uses common across the study area. The elevation ranges from sea level to 1,917 m (Mt. Washington) with a range of topographies from coastal plains, foothills, mountain ranges (Appalachian and Laurentian), glacial landscapes of the Great Lakes region, and plains and river valleys of the Ohio and Mississippi rivers. The Köppen-Geiger climate zones (1975–2000) include temperate fully humid, hot summer, temperate fully humid, warm summer, cold fully humid hot summer, cold fully humid, warm summer, and cold fully humid, cool summer. Our modeled taxa, and most North American salamander species, are forest specialists that occur in lowland forest stands and, in the case of bi-phasic species, near isolated wetlands (Davic and Welsh 2004). Related species that are found within the study area and may compete with our modeled taxa include the northern slimy salamander (*Plethodon glutinosus*), the small-mouthed salamander (*Ambystoma texanum*), the eastern tiger salamander (*Ambystoma tigrinum*), and the Jefferson salamander (*Ambystoma jeffersonianum*).

METHODS

Species data

We obtained occurrence datasets for each species from the Global Biodiversity Information Facility (2020). To improve spatial and temporal accuracy of species localities, we removed coordinates with <4 decimal places (i.e., spatial uncertainty >1,000 m) and collection dates prior to 1960 to correspond with current climate conditions (Milanovich et al. 2012, Préau et al. 2018). We clipped species occurrence datasets to remove confounding records using shapefiles representing the known ranges of each species (Anderson and Raza 2010, International Union for Conservation of Nature [IUCN] 2020).

Presence-only modeling methods are sensitive to spatially autocorrelated (i.e., non-independent) occurrence data (Veloz 2009). Spatial autocorrelation of occurrence data is inherent based on species habitat preferences, but it is also a symptom of biased sampling regimes (e.g., dense localities in nature parks) from which biodiversity database localities suffer (Shcheglovitova and Anderson 2013). To increase the proportion of spatially independent localities in species datasets, we removed duplicate observations and buffered remaining localities at 1 km in SDMToolbox version 2.4 (Brown 2014). Spatially rarefying occurrences also reduced the chance of overfitting models on sample values from areas of highly clustered points (e.g., National Parks, biological stations). We selected a buffer of 1 km to align with the maximum dispersal distance of organisms modeled and to limit the maximum number of localities per map pixel (Phillips and Dudík 2008).

Climate data

We obtained high-resolution (30-arcseconds) climatic layers from the WorldClim database (Hijmans et al. 2005). WorldClim provides datasets consisting of 19 bioclimatic variables purported as biologically relevant in that they represent climate processes known to limit distributions of climate-sensitive species (e.g., max. temp of warmest month). Datasets representing current climate conditions are derived from monthly temperature and precipitation values representative of a temporal scale of 1960–2000. We clipped climate raster files to the study region (i.e., MaxEnt extent) of each species in ArcMap version 10.7 (Esri, Redlands, CA, USA).

To predict future changes in climate niches, environmental data predicted for specific future climate change scenarios are required (Pearson and Dawson 2003). The Climate Change, Agriculture, and Food Security data portal (<http://ccafs-climate.org>, accessed 5 Oct 2021) provides datasets of climatic variables developed for use in climate change impact assessments on agriculture and biodiversity. Using the delta change method, Navarro-Racines et al. (2020) quantified anomalies in predictions between baseline and future projections which were then interpolated onto a grid and applied to the WorldClim baseline data. Correcting the modeled mean climate from global climate models (GCM) allows for impacts of climate change at smaller scales to be shown in models (Hawkins et al. 2013).

From the Climate Change, Agriculture, and Food Security portal, we obtained bioclimatic variable datasets representing 2 time periods (2050, 2070), 2 widely used GCMs (HadGEM2-ES, CCCMA-CanESM2), and 2 representative concentration pathways (RCP 4.5 and RCP 8.5) at a resolution of 0.000833DD (i.e., ~1 km²). Representative concentration pathways (RCP) are estimates of radiative forcing (W/m) corresponding with different atmospheric carbon dioxide concentrations (Intergovernmental Panel on Climate Change [IPCC] 2007). We included climate projections under 2 different GCMs to account for variability in model results that can arise from differences in the mathematical processes used to develop GCMs (Semenov and Stratonovitch 2010). Including climate scenarios associated with stabilizing (RCP 4.5) and increasing (RCP 8.5) atmospheric greenhouse gas concentrations may provide insight to how mitigating global carbon dioxide emissions may abate climate change impacts on sensitive taxa.

Niche modeling in MaxEnt

We used the maximum entropy method, MaxEnt version 3.4.4., to run tuning models and fit current models that we subsequently projected into future climate scenarios (Phillips et al. 2006). While many algorithms have been used to model species distributions (e.g., MaxEnt, ecological niche factor analysis, genetic algorithm for rule set production, random forest, DOMAIN), they all seek to identify the environmental conditions in which a species is most likely to occur (Ortega-Huerta and Peterson 2008, Evans et al. 2011, Peterson et al. 2017). The presence-background method employed by MaxEnt selects background points (i.e., pseudoabsences) within a user-defined region to be tested against presence points used for model building to characterize environmental conditions in regions where species exist versus where they are suspected to be absent (Phillips 2005). By default, MaxEnt randomly selects 10,000 points across the study region to be used as pseudoabsences. Some have criticized the random background point selection method used by MaxEnt because it can lead to the selection of points in unsampled areas occupied by target organisms or regions with suitable conditions yet to be colonized by the modeled species (Kramer-Schadt et al. 2013). Ensuring background points are selected from areas where the target species is known to be absent is important to developing useful models (Engler et al. 2004). Lack of consideration for background point selection can potentially result in high false-positive rates (commission errors) and low model predictive power (Halvorsen et al. 2016).

We used 2 methods to promote the selection of informative pseudoabsences: using geographic extents for current model calibration smaller than those of future projections and defining background regions with bias files. Using a larger study area for MaxEnt modeling increases the risk of throw-away background points being selected because probability of unoccupied, biologically suitable areas decreases with distance from the known niche of a target organism (Barbet-Massin et al. 2012). Using IUCN range maps, we defined the study areas (i.e., MaxEnt extent) for fitting models of each individual species (Anderson and Raza 2010). Bias files define areas of high-density sampling and control where, in the study region, background points should be selected (Brown et al. 2017). To define the regions of background point selection, we used a minimum convex polygon around full occurrence datasets buffered at 1 km.

To select the regularization multiplier value and set of environmental variables to be used in final model construction, we implemented a tuning process based on Raghavan et al. (2019). Following the release of MaxEnt software, publications reporting the effects of sample size, variable resolution, and various parameterizations (e.g., regularization multiplier [RM] values, feature classes) on resulting model accuracy aimed to provide general guidelines to MaxEnt users (Baldwin et al. 2006, Hernandez et al. 2006, Franklin 2010). Despite this, a lack of consideration for problematic implementations of the software made known in early MaxEnt publications are evident in MaxEnt modeling literature. The RM in MaxEnt is used to limit model complexity, thus preventing overfitting (Phillips et al. 2006). Increasing the RM used in model calibration can result in models with more spread-out species distributions (Baldwin 2009). We used a tuning procedure for each species using all combinations of 8 RM values (0–4 at intervals of 0.5) and 3 distinct variable groupings with 5 cross-validation replicates each with a random seed. We tested multicollinearity among variables in each species' full climate dataset (19 variables) and formed a set of biologically relevant, uncorrelated variables for the first grouping. For the second variable grouping, we compiled variables absent from the initial grouping then, using variables that showed significant contribution in tuning models built with the first and second groupings, we created the third grouping. Variable groupings included at most 8 variables (i.e., $n/K > 10$, where K = number of variables), none of which were correlated (e.g., $r > 0.85$; Elith et al. 2010). This variable filtering process allowed for the consideration of variables that may not have been identified as critical to the species' climatic niche and expanded the number of variables tested for model contribution.

Using 3 variable groupings, 8 RMs, and 4 species, we calibrated 96 unique tuning models in the MaxEnt Windows graphical user interface (version 3.4.1) with 5-fold cross validation, random seeds, and ≤ 500 iterations. We evaluated tuning models using the test area under the operating characteristic curve (AUC_{Test}), test omission

rate (based on a 10% training presence threshold), and the sample size corrected Akaike's Information Criterion (AIC_c), in that order (Raghavan et al. 2019). Of the 480 runs, we retained 118 (39%) that showed reasonable performance against random (i.e., $AUC_{\text{Test}} \geq 0.70$) and test omission values equal to or less than the theoretical threshold value of 10% (i.e., omission rate ≤ 0.10). Using raster and rmaxent packages in R 4.0.2, we calculated ΔAIC_c of remaining models and identified top models as those with ΔAIC_c values of zero (Hijmans et al. 2015, R Development Core Team 2017). After the tuning evaluation process, we selected an RM of 0.5 for the red-backed salamander, blue-spotted salamander, and spotted salamander and an RM of 2 for the four-toed salamander. We selected the first variable grouping for the blue-spotted salamander and four-toed salamander, the second for the red-backed salamander, and the third for the spotted salamander (Table 1).

Model evaluation and analysis

We fit final niche models for each species and projected models to 8 future climate scenarios with parameters (RM value and environmental variable grouping) selected by each tuning procedure. By default, MaxEnt uses linear, quadratic, product, and hinge features for calculating species responses to environmental variables. We selected linear and quadratic features for model creation to avoid the creation of biologically unrealistic species response curves and to reduce the amount of clamping that must be performed by MaxEnt as models are being transferred spatially and temporally (Glon et al. 2017). We set MaxEnt to run 10-fold subsample replications using a random test percentage of 30 with random seeds and ≤ 500 iterations.

To account for the effect threshold criteria may have on model outputs, we evaluated final models using threshold-dependent and threshold-independent measures (Freeman and Moisen 2008). The area under the

TABLE 1 A culmination of the bioclimatic variables used to build current (1960–1990) and future (2041–2060 and 2061–2080) climatic niche models for the spotted salamander, blue-spotted salamander, four-toed salamander, and red-backed salamander in eastern United States and Canada. We present the climate factors from the variable groupings selected for MaxEnt model calibration. We did not use the 14 variables listed together in modeling each individual species, yet we compiled variables within groupings selected in the tuning procedure.

Bioclimatic variable	Variable description
BIO 1	Annual \bar{x} temp
BIO 2	\bar{x} diurnal range (\bar{x} monthly [max. temp – min. temp])
BIO 3	Isothermality (\bar{x} diurnal range/temp annual range) $\times 100$
BIO 4	Temp seasonality ($SD \times 100$)
BIO 5	Max. temp of warmest month
BIO 6	Max. temp of coldest month
BIO 8	\bar{x} temp of wettest quarter
BIO 10	\bar{x} temp of warmest quarter
BIO 12	Annual precipitation
BIO 13	Precipitation of wettest month
BIO 14	Precipitation of driest month
BIO 15	Precipitation seasonality (coefficient of variation)
BIO 16	Precipitation of wettest quarter
BIO 18	Precipitation of warmest quarter

receiver operating characteristic curve (AUC) calculated by MaxEnt is a threshold-independent measure that can be interpreted as the probability a random presence or a random absence (i.e., background point) is classified correctly (Phillips and Dudík 2008). An AUC of 0.5 indicates random model performance (i.e., no discriminant capacity) and a value >0.7 indicates reasonable model performance (Pearce and Ferrier 2000). We included the minimum difference between training and test AUC values (AUC_{Diff}) as a measure of overfitting on training data (Warren and Seifert 2011). To quantify robustness of results, we included the standard deviation of test AUC across model replicates (AUC_{SD} ; Elith and Leathwick 2007). The implementation of AUC by MaxEnt differs from the typical application of the measure in presence or absence analyses (Konowalik and Nosol 2021).

The 10% training presence threshold rule applied to niche models selects the value that excludes 10% of test localities with the lowest predicted presence probability so ideal models return 10% (i.e., 0.10) omission rates on test data (Jarnevich and Reynolds 2011). We selected the 10% training presence threshold because it is less sensitive to extreme or outlier localities that may be present in datasets from biodiversity databases and can permeate the rarefaction process mentioned above (Beck et al. 2014). The 10% training presence threshold rule we applied to final models and projections constitutes a less permissive condition for making binary distribution predictions and is used alongside species data collected over long periods of time (Rebelo et al. 2010). We consolidated binary model predictions using a fuzzy overlay tool in ArcMap and then calculated the spatial shifts of species climatic niches' using a raster math tool in SDMToolbox. To visualize trends in climatic range shifts under climate change, we present maps displaying regions of range contraction, retention (i.e., no change), and expansion as predicted by each projected model.

To evaluate range restriction for each species, we quantified the proportions of occurrences falling in climatically suitable regions (i.e., positivity rates) in current and future binary models. Before comparing positivity rates of models under current conditions against projected models, we used a fuzzy overlay tool with an AND operator to combine predictions across replicates and then across the 2 global climate models. This reduced the number of future climate scenarios from 8 (2 GCMs, 2 RCPs, and 2 time periods) to 4 (2 RCPs and 2 time periods) per species. We used the extract values to points tool in ArcMap to find raster values of species localities where zero was unsuitable (i.e., negative) and 1 was suitable (i.e., positive). After calculating the proportion of localities classified as positive in current and future models, we determined the difference between values for current models and those under our 4 future climate scenarios.

RESULTS

We assessed final current niche models for potential over- and under-fitting with the AUC for training (AUC_{Train}) and test data (AUC_{Test}), mean deviation of AUC per observation, minimum difference between training and test AUC (AUC_{Diff}), and test omission rate. Test AUC values across species models ranged from 0.72 (spotted salamander) to 0.78 (blue-spotted salamander), indicating fair model performance (Swets 1988). Model results from the blue-spotted salamander, spotted salamander, and red-backed salamander were robust in terms of AUC on test localities (i.e., $AUC_{SD} < 0.05$), not overfit on training data when compared to test data (AUC_{Diff}) and performed better than random as suggested by test omission rates. By common standards, the four-toed salamander models would not be considered overfit, but robustness was slightly decreased when comparing AUC results ($AUC \pm 0.035$ [SD]) and omission rate (0.137) to those of the 3 other species (Table 2).

We calculated and compared occurrence positivity rates between models under current and future climatic conditions to show the severity of range restriction as time and greenhouse gas emissions increased. Models under current conditions predicted occurrence positivity rates of 87% (548 of 630 points) for the blue-spotted salamander, 88% (1,349 of 1,526 points) for the spotted salamander, 83% (115 of 138 points) for the four-toed salamander, and 88% (2,748 of 3,114 points) for the red-backed salamander (Figure 1). Models projected under

TABLE 2 Results of threshold-independent (area under the receiver operating characteristic curve [AUC]) and threshold-dependent (omission rate) analyses on current (1960–1990) climatic niche models for the spotted salamander, blue-spotted salamander, four-toed salamander, and red-backed salamander in eastern United States and Canada.

Species	n^a	AUC _{Train} ^b	AUC _{Test} ^c	AUC SD (\pm)	AUC _{Diff} ^d	Omission rate
Spotted salamander	1,069	0.728	0.730	0.011	0.0016	0.097
Blue-spotted salamander	440	0.787	0.783	0.016	0.0021	0.114
Four-toed salamander	97	0.778	0.720	0.035	0.0001	0.137
Red-backed salamander	2,180	0.726	0.725	0.008	0.0001	0.100

^aNumber of occurrences used to develop models.

^bArea under the receiver operating characteristic on training localities.

^cArea under the receiver operating characteristic on test localities.

^dThe minimum difference between training and test AUC among model replicates.

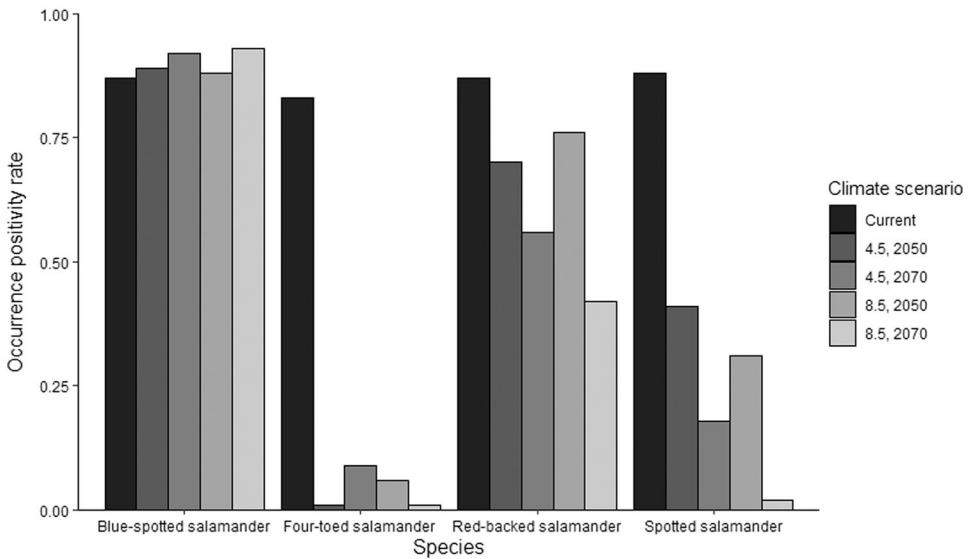


FIGURE 1 Occurrence positivity rates from current (1960–1990) and future (2041–2060 and 2061–2080) climatic niche models for the spotted salamander, blue-spotted salamander, four-toed salamander, and red-backed salamander in eastern United States and Canada. Values represent the proportions of occurrences falling in climatically suitable regions as time period (2050 and 2070) and greenhouse gas concentrations (RCP 4.5 and RCP 8.5) were varied (i.e., scenario 2050 + RCP4.5 simulates climatic conditions expected by the mid-century if emissions follow the intermediate representative concentration pathway, RCP 4.5).

future conditions predicted average positivity rates of 91% (89–93%) for the blue-spotted salamander, 23% (2–41%) for the spotted salamander, 4% (0.7–9%) for the four-toed salamander, and 61% (42–76%) for the red-backed salamander (Figure 1).

We quantified shifts in climatic suitability across species' known ranges predicted under 4 future climate scenarios (Figures 2–5). We determined changes in climatically suitable area by overlaying current binary models with projected binary models and calculating the regions where suitability is expected to increase, decrease, or

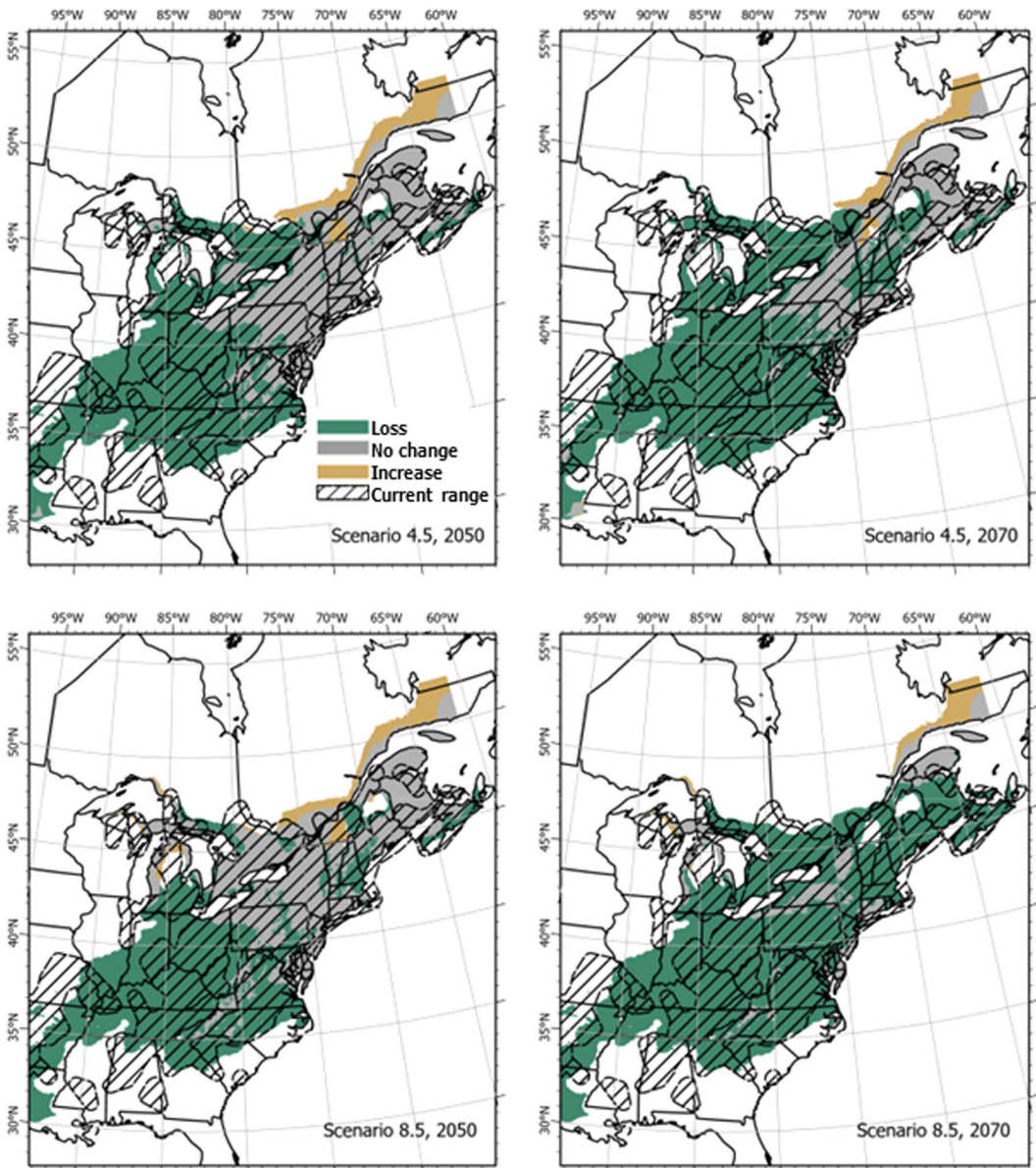


FIGURE 2 Change in climatic suitability in eastern United States and Canada for the spotted salamander under 4 future (2041–2060 and 2061–2080) climate change scenarios. Maps display regions of range loss (green), no change (grey), and range expansion (brown) predicted to occur under 4 scenarios of continued climate change. The dashed-line polygons represent species current (1960–1990) ranges as defined by Global Biodiversity Information Facility observations. Each scenario is a unique combination of one time period (2050 and 2070) and 1 greenhouse gas concentration trajectory (4.5 and 8.5; where 4.5 is intermediate and 8.5 is extreme).

remain. Using maps (Figures 2–5) under equal area projections, we calculated the amount of climatically suitable area for each species under current and future models (Table 3). From projected species models, we observed declines in suitable area for the spotted salamander, four-toed salamander, and red-backed salamander, and net increases in suitable area for the blue-spotted salamander.

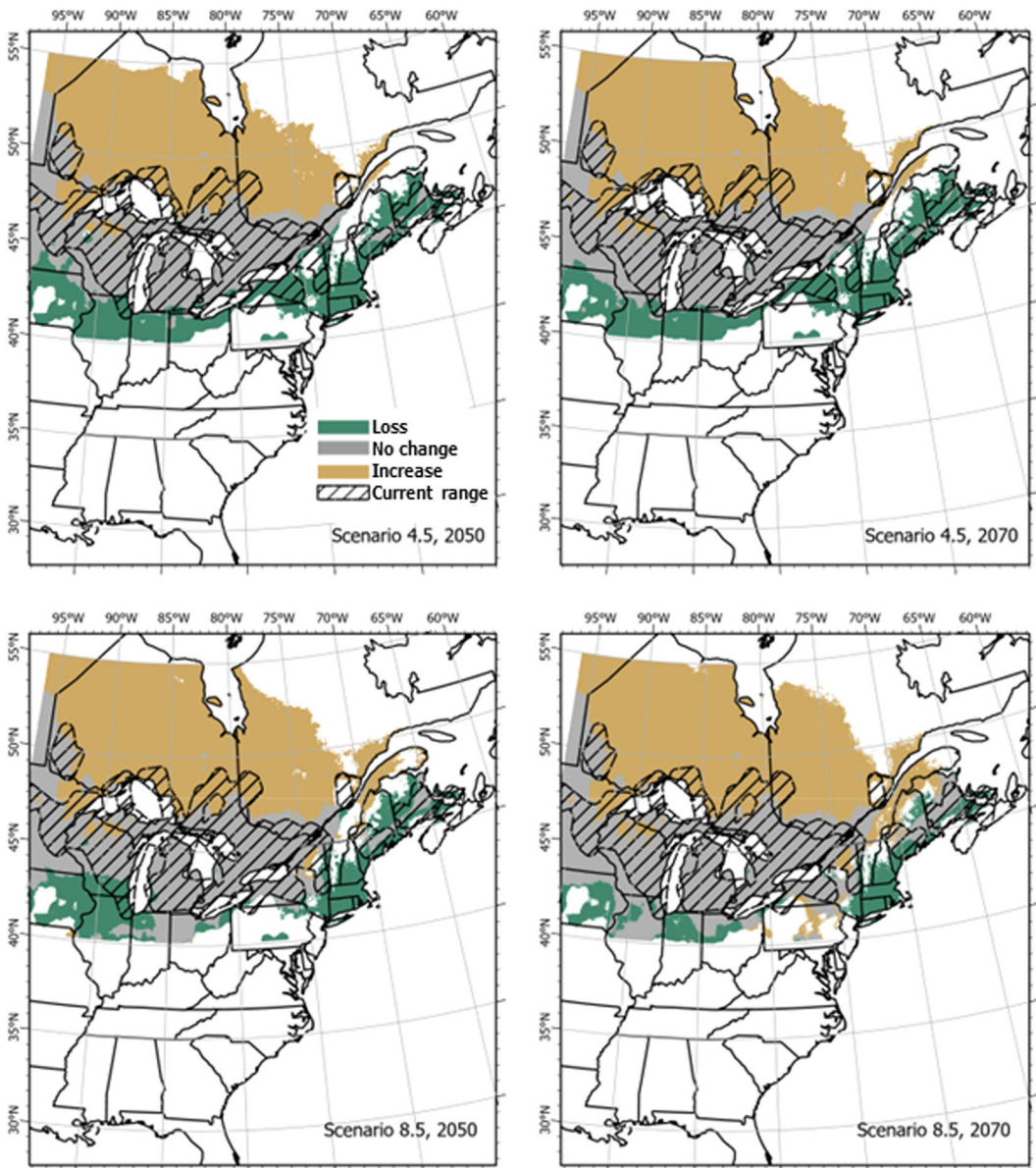


FIGURE 3 Change in climatic suitability in eastern United States and Canada for the blue-spotted salamander under 4 future (2041–2060 and 2061–2080) climate change scenarios. Maps display regions of range loss (green), no change (grey), and range expansion (brown) predicted to occur under 4 scenarios of continued climate change. The dashed-line polygons represent species current (1960–1990) ranges as defined by Global Biodiversity Information Facility observations. Each scenario is a unique combination of one time period (2050 and 2070) and 1 greenhouse gas concentration trajectory (4.5 and 8.5; where 4.5 is intermediate and 8.5 is extreme).

DISCUSSION

We hypothesized that by forecasting climatic niche models of 4 common salamander species into moderate and extreme climate change scenarios, we would observe significant reductions in suitable habitat across species' geographic ranges. Indeed, forecasted climate models predicted reductions in suitable climatic range for all species

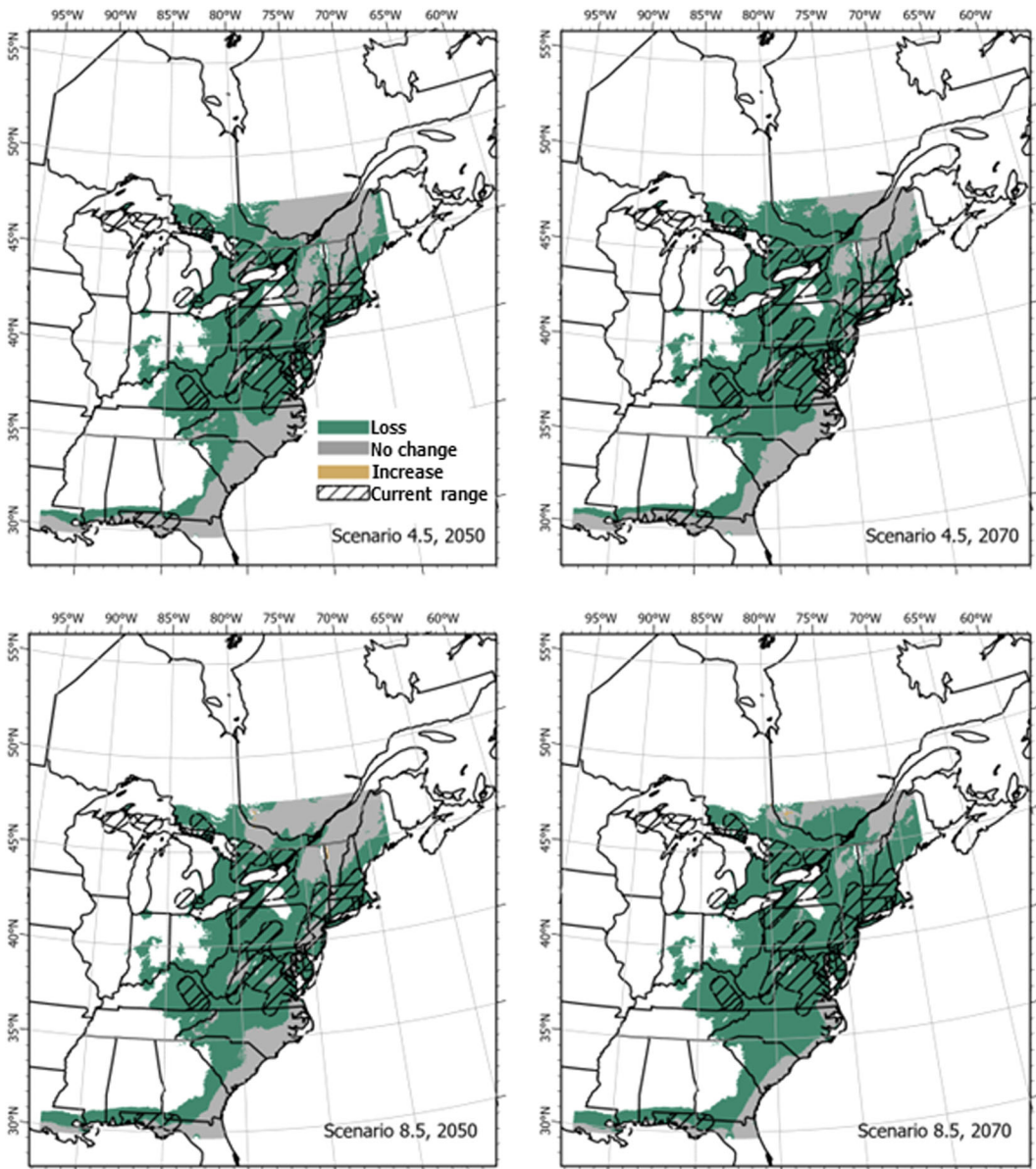


FIGURE 4 Change in climatic suitability in eastern United States and Canada for the four-toed salamander under 4 future (2041–2060 and 2061–2080) climate change scenarios. Maps display regions of range loss (green), no change (grey), and range expansion (brown) predicted to occur under 4 scenarios of continued climate change. The dashed-line polygons represent species current (1960–1990) ranges as defined by Global Biodiversity Information Facility observations. Each scenario is a unique combination of one time period (2050 and 2070) and 1 greenhouse gas concentration trajectory (4.5 and 8.5; where 4.5 is intermediate and 8.5 is extreme).

but to varying degrees. We observed the greatest reductions in climatic range for the spotted salamander, four-toed salamander, and red-backed salamander with reductions in positive localities of -65% , -79% , and -27% averaged across future models. Alternatively, projected blue-spotted salamander models displayed less range restriction and an increased amount of climatic range expansion when compared to the current model. While all

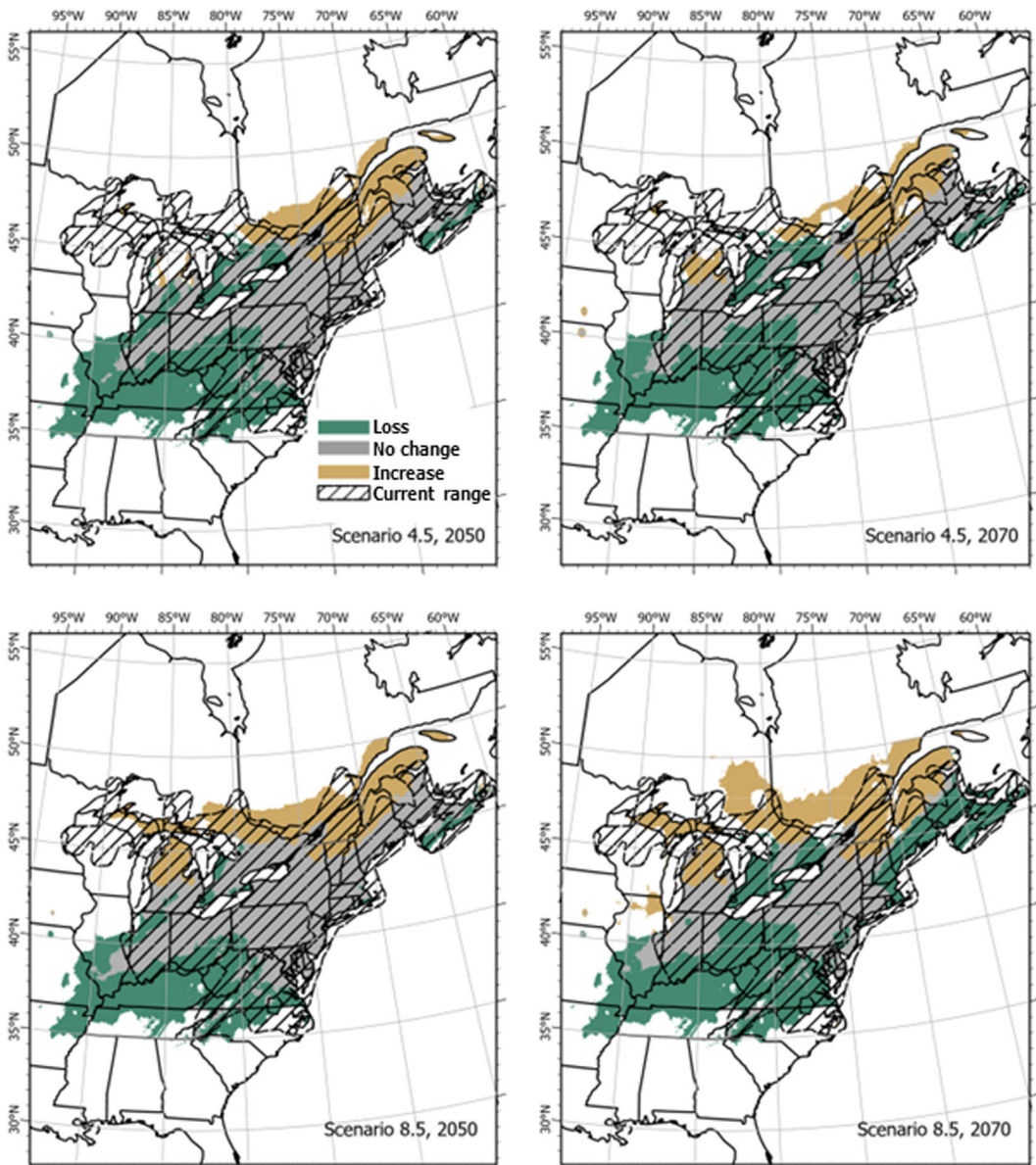


FIGURE 5 Change in climatic suitability in eastern United States and Canada for the red-backed salamander under 4 future (2041–2060 and 2061–2080) climate change scenarios. Maps display regions of range loss (green), no change (grey), and range expansion (brown) predicted to occur under 4 scenarios of continued climate change. The dashed-line polygons represent species current (1960–1990) ranges as defined by Global Biodiversity Information Facility observations. Each scenario is a unique combination of 1 time period (2050 and 2070) and 1 greenhouse gas concentration trajectory (4.5 and 8.5; where 4.5 is intermediate and 8.5 is extreme).

species models showed potential future range expansion, we suggest this result be considered cautiously as our models only factor in climate and were not parameterized with all environmental conditions that make habitat suitable for salamanders (e.g., presence of wetlands, land cover, forest type) or enable the exploitation of newly suitable habitat (e.g., habitat connectivity, dispersal rate; Lawler et al. 2010). Thus, our results, primarily predicting

TABLE 3 Area of climatically suitable habitat in eastern United States and Canada predicted for the blue-spotted salamander, spotted salamander, red-backed salamander, and four-toed salamander under current (1960–1990) and future (2041–2060 and 2061–2080) climatic scenarios (4.5 and 8.5 indicate atmospheric greenhouse gas concentrations, where 4.5 is intermediate and 8.5 is extreme).

Species	Current climatic range (km ²)	Future range: 2050 4.5 (km ²)	Future range: 2070 4.5 (km ²)	Future range: 2050 8.5 (km ²)	Future range: 2070 8.5 (km ²)
Spotted salamander	1,946,111.87	874,229.77	587,914.88	941,598.40	307,992.28
Blue-spotted salamander	1,339,672.94	1,929,373.16	2,053,567.80	2,203,864.83	2,386,794.49
Four-toed salamander	1,438,867.41	537,268.91	436,415.73	472,334.84	237,530.95
Red-backed salamander	1,387,647.13	1,008,414.12	952,786.67	1,269,206.27	1,086,291.49

reduction with limited expansion of climatically suitable habitat for salamanders under climate change, are consistent with findings of climate modeling studies focused on amphibian taxa (Barrett et al. 2014, Sutton et al. 2015, Struecker and Milanovich 2017).

Climatic range restriction

By calculating differences in occurrence positivity rates (Figure 1) and developing range shift maps (Figures 2–5), we showed the severe impacts continued climate change may have on the historically wide climatic ranges of the spotted salamander, blue-spotted salamander, four-toed salamander, and red-backed salamander. We included multiple future climate scenarios by varying time period and atmospheric greenhouse gas concentration to understand how climate change mitigation (RCP 4.5), or lack thereof (RCP 8.5), may influence climatic range loss in coming decades. In agreement with our hypothesis, climatic range restriction peaked in models projected into the latest and highest concentration climate scenario (i.e., 2070 + RCP 8.5). Comparing contemporary models with those under the 2070 + RCP 8.5 scenario, 86.5%, 83%, and 46% of occurrence points were predicted to fall in climatically unsuitable regions for the spotted salamander, four-toed salamander, and red-backed salamander, respectively (Figure 1). Our results align with those of similar studies with closely related modeled taxa in that southern range limits register the greatest reduced climatic suitability and climatic range restriction increases with time and atmospheric greenhouse gas concentration (Buermann et al. 2008, Chen et al. 2011).

While the focus of this study was climatic range restriction, we observed a wide range of climatic range expansion predicted across all projected species models. Change in climatic range maps show negligible amounts of range expansion predicted for the spotted salamander and four-toed salamander (Figures 2 and 4), while the notable amount of expansion predicted for the blue-spotted salamander and red-backed salamander increased with time and greenhouse gas concentration (Figures 3 and 5). Predicted climatic range expansion was concentrated in regions north of the blue-spotted salamander's and red-backed salamander's native ranges, but it was evident that current niche models of both species underpredicted suitability near northern range limits. As a result, some regions classified as newly suitable (i.e., expansion) in future models are currently occupied by modeled species. In their study using climate and land-use features to assess the spatial patterns of cold-adapted amphibians, Seaborn et al. (2021) reported climate-only and combination ecological niche models underpredicted the northern edge for high latitude species. Similarly, we suggest underpredicted suitability in northern range limits of current models, sampling bias in occurrence collections, and spatial filtering of localities influenced the climatic range expansion observed for our 2 high-latitude species (blue-spotted salamander and red-backed salamander; Sheridan et al. 2018).

Niche-breadth and model predictions

To understand how forecasted climate impacts vary with species' geographic extents, we included 4 species with comparable northerly range limits (southern Ontario and Quebec, Canada): 2 occurring throughout the eastern United States (spotted salamander and four-toed salamander) and 2 limited to higher latitudes of the same region (blue-spotted salamander and red-backed salamander). The blue-spotted salamander, found as far south as northern Indiana, USA, has the northern-most range of all North American salamanders and the red-backed salamander extends slightly farther south reaching South Carolina (Demastes et al. 2007). As hypothesized, the spotted salamander and four-toed salamander were projected to lose greater quantities of climatic range than the blue-spotted salamander and red-backed salamander in each future climate scenario (Table 3). These results coincide with modeling research that suggests species niche breadth and distribution are important predictors of responses to changing climate conditions and habitat alterations (Swihart et al. 2003, Connor et al. 2018).

We demonstrate that when only considering changing climatic conditions, widely distributed salamanders of the eastern United States and Canada are expected to face large-scale range restriction by the mid to late twenty-first century. Salamanders are sensitive to a long list of environmental variables outside of climate and multiple studies have suggested certain factors (e.g., competition, fragmentation) will compound with changing climate patterns to further restrict species ranges and prohibit exploitation of newly suitable habitat (Godsoe et al. 2017, Lewis et al. 2017). For example, our pond-breeding species (spotted salamander, blue-spotted salamander, and four-toed salamander) cannot persist or establish populations in areas lacking wetlands, a limitation that could in theory improve estimates of suitable habitat distribution (Homan et al. 2004, Ryan and Calhoun 2014). Unfortunately, the availability of high-quality topographic and geographic datasets is limited in part because of the complexity of quantifying features at fine scales, synthesizing data across large areas, and projecting estimates to future time periods. The availability of high-resolution future climate data sets and the importance of climatic conditions in determining suitable habitat for amphibian taxa make climate-only modeling a viable tool for estimating species responses to anthropogenic climate change (Searcy and Schaffer 2016).

Addressing methodologies

In interpreting niche model results, it is important to address methodologies used in model development and evaluation that have received conflicting support in the literature. First, use of AUC as an indication of niche model quality has been criticized specifically when applied to presence-only modeling methods (Peterson et al. 2008). The goal of the AUC is to compare the discriminatory ability (i.e., predicting presences and absences correctly) of a classification model against random (Hosmer and Lemeshow 1980). One issue with the AUC is, as a comparison against random, accurate models of widespread generalist species will return low AUC values compared to specialist species (Lobo et al. 2008). Another issue with AUC in presence-only modeling stems from the potential for pseudoabsences (i.e., background data) to fall in regions that are suitable to or inhabited by the modeled species (Jiménez-Valverde 2012). Additionally, the use of AIC in evaluating MaxEnt models has been criticized with simulated studies reporting a tendency for AIC to select models with high commission and omission errors (Velasco and González-Salazar 2019). We addressed the issue of problematic background data by using a bias file to increase the proportion of informative pseudoabsences (Brown et al. 2017). In evaluating tuning and final models with omission rate and compliments to AUC (SD of AUC and minimum difference between training and test AUC values), we attempted to correct for the selection of undesirable model qualities using AIC, quantify overfitting, and represent deviation of fitted values across observations (Baldwin 2009, Radosavljevic and Anderson 2014, Zhang et al. 2020). Finally, the purpose of the tuning procedure used, in part, to select variables and regularization multiplier values for model construction was to remove the inherent ambiguity involved in standard model parameterization practices evident from comparable literature. The statistical evaluation implemented to filter tuning runs may not have been fit for selecting adequately parameterized models (i.e., multiple highly contributing variables) but, instead, fit for selecting models exhibiting discriminatory capacity and lack of over-fitting.

Overall, our analyses suggest 4 salamander species common across the eastern United States and Canada will experience dramatic range restrictions in response to anthropogenic climate change. While a plethora of factors outside climate (e.g., land use, species interactions, human footprint) influence habitat suitability (Heikkinen et al. 2007), researchers report that climate-only niche models, especially for amphibian taxa, can perform similarly or better than combination models (Bucklin et al. 2015, Seaborn et al. 2021). By calibrating models with multiple estimations of atmospheric greenhouse gas concentrations, we showed that even a drastic reduction in global emissions will not save the taxa modeled from significant climatic range restrictions.

CLIMATE CHANGE IMPLICATIONS

Continually shifting climate patterns (i.e., hydroperiod, severe temperature and precipitation events) negatively affect aquatic breeding success, increase physiological stress in juveniles and adults, and will lead to local extinctions of salamander populations. Our models can be used by managers and conservation planners at local and landscape scales to identify potential suitable habitat with climate change and habitat linkages required to maintain connectivity. In addition to the negative impacts of broad-scale factors such as climate, species ranges will also experience reductions in suitable habitat in response to changes in localized factors such as pollution and community structure. Losing common taxa to climatic stress can increase vulnerability of ecosystems to perturbation and lead to deterioration in community structure, trophic-level synchrony, and biodiversity. To avoid the significant ecological implications associated with the loss of common species, further research, population monitoring, and management projects must reject the complacency that exists with the conservation of widespread taxa.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Species data used in this study were acquired from the open-access database, Global Biodiversity Information Facility, and the authors did not sample or handle specimens to collect data. No permits were required to conduct the research outlined in this article.

DATA AVAILABILITY STATEMENT

Occurrence records are available from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>, accessed 5 Oct 2021). Raster layers representing species geographic ranges are available from the IUCN Red List website (<https://www.iucnredlist.org/resources/spatial-data-download>, accessed 22 Oct 2021). Raster layers of climatic variables are available from the WorldClim database (<https://www.worldclim.org>, accessed 5 Oct 2021) and the Climate Change, Agriculture, and Food Security database (CCAFS; <http://ccafs-climate.org>, accessed 5 Oct 2021).

ORCID

Brian W. Widmer  <http://orcid.org/0000-0002-2260-875X>

REFERENCES

- Anderson, R. P., and A. Raza. 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography* 37:1378–1393.
- Baldwin, R. A. 2009. Use of maximum entropy modeling in wildlife research. *Entropy* 11:854–866.
- Baldwin, R. F., A. J. K. Calhoun, and P. G. deMaynadier. 2006. The significance of hydroperiod and stand maturity for pool-breeding amphibians in forested landscapes. *Canadian Journal of Zoology* 84:1604–1615.
- Banning, J. L., A. L. Weddle, G. W. Wahl, III, M. A. Simon, A. Lauer, R. L. Walters, and R. N. Harris. 2008. Antifungal skin bacteria, embryonic survival, and communal nesting in four-toed salamanders, *Hemidactylium scutatum*. *Oecologia* 156:423–429.
- Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* 3:327–338.
- Barrett, K., N. P. Nibbelink, and J. C. Maerz. 2014. Identifying priority species and conservation opportunities under future climate scenarios: amphibians in a biodiversity hotspot. *Journal of Fish and Wildlife Management* 5:282–297.
- Beck, J., M. Böller, A. Erhardt, and W. Schwanghart. 2014. Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecological Informatics* 19:10–15.
- Brown, J. L. 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution* 5:694–700.
- Brown, J. L., J. R. Bennett, and C. M. French. 2017. SDMtoolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ* 5:e4095.
- Brown, J. L., N. Sillero, F. Glaw, P. Bora, D. R. Vieites, and M. Vences. 2016. Spatial biodiversity patterns of Madagascar's amphibians and reptiles. *PLoS One* 11:e0144076.
- Bucklin, D. N., M. Basille, A. M. Benscoter, L. A. Brandt, F. J. Mazzotti, S. S. Romañach, C. Speroterra, and J. I. Watling. 2015. Comparing species distribution models constructed with different subsets of environmental predictors. *Diversity and Distributions* 21:23–35.
- Buermann, W., S. Saatchi, T. B. Smith, B. R. Zutta, J. A. Chaves, B. Milá, and C. H. Graham. 2008. Predicting species distributions across the Amazonian and Andean regions using remote sensing data. *Journal of Biogeography* 35: 1160–1176.
- Cabe, P. R., R. B. Page, T. J. Hanlon, M. E. Aldrich, L. Connors, and D. M. Marsh. 2007. Fine-scale population differentiation and gene flow in a terrestrial salamander (*Plethodon cinereus*) living in continuous habitat. *Heredity* 98:53–60.
- Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
- Connor, T., V. Hull, A. Viña, A. Shortridge, Y. Tang, J. Zhang, F. Wang, and J. Liu. 2018. Effects of grain size and niche breadth on species distribution modeling. *Ecography* 41:1270–1282.
- Davic, R. D., and H. H. Welsh, Jr. 2004. On the ecological roles of salamanders. *Annual Review of Ecology, Evolution & Systematics* 35:405–434.
- Demastes, J. W., J. M. Eastman, and J. S. East. 2007. Phylogeography of the blue-spotted salamander, *Ambystoma laterale* (Caudata: Ambystomatidae). *American Midland Naturalist* 157:149–161.
- Earl, J. E., T. M. Luhring, B. K. Williams, and R. D. Semlitsch. 2011. Biomass export of salamanders and anurans from ponds is affected differentially by changes in canopy cover. *Freshwater Biology* 56:2473–2482.
- Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution* 1:330–342.
- Elith, J., and J. Leathwick. 2007. Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity and Distributions* 13:265–275.
- Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* 41:263–274.
- Esser, L. F., D. M. Neves, and J. A. Jarenkow. 2019. Habitat-specific impacts of climate change in the Mata Atlântica biodiversity hotspot. *Diversity and Distributions* 25:1846–1856.
- Evans, J. S., M. A. Murphy, Z. A. Holden, and S. A. Cushman. 2011. Modeling species distribution and change using random forest. Pages 139–159 in C. A. Drew, Y. F. Wiersma, and F. Huettmann, editors. *Predictive species and habitat modeling in landscape ecology*. Springer, New York, New York, USA.
- Fitzpatrick, M. C., A. D. Gove, N. J. Sanders, and R. R. Dunn. 2008. Climate change, plant migration, and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia. *Global Change Biology* 14:1337–1352.
- Flesch, A. D. 2019. Patterns and drivers of long-term changes in breeding bird communities in a global biodiversity hotspot in Mexico. *Diversity and Distributions* 25:499–513.
- Franklin, J. 2010. *Mapping species distributions: spatial inference and prediction*. Cambridge University Press, Cambridge, United Kingdom.

- Freeman, E. A., and G. G. Moisen. 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling* 217:48–58.
- Gaston, K. J. 2010. Valuing common species. *Science* 327:154–155.
- Global Biodiversity Information Facility. 2020. GBIF occurrence download. <<https://doi.org/10.15468/dl.664k8g>>, <<https://doi.org/10.15468/dl.aknqc8>>, <<https://doi.org/10.15468/dl.8a38fy>>, <<https://doi.org/10.15468/dl.r6ncrp>>. Accessed 5 Oct 2020.
- Glon, H. E., B. W. Heumann, J. R. Carter, J. M. Bartek, and A. K. Monfils. 2017. The contribution of small collections to species distribution modelling: a case study from Fuireneae (Cyperaceae). *Ecological Informatics* 42:67–78.
- Godsoe, W., J. Franklin, and F. G. Blanchet. 2017. Effects of biotic interactions on modeled species' distribution can be masked by environmental gradients. *Ecology and Evolution* 7:654–664.
- Halvorsen, R., S. Mazzoni, J. W. Dirksen, E. Næsset, T. Gobakken, and M. Ohlson. 2016. How important are choice of model selection method and spatial autocorrelation of presence data for distribution modelling by MaxEnt? *Ecological Modelling* 328:108–118.
- Harris, R. N., and P. M. Ludwig. 2004. Resource level and reproductive frequency in female four-toed salamanders, *Hemidactylum scutatum*. *Ecology* 85:1585–1590.
- Hawkins, E., T. M. Osborne, C. K. Ho, and A. J. Challinor. 2013. Calibration and bias correction of climate projections for crop modelling: an idealised case study over Europe. *Agricultural and Forest Meteorology* 170:19–31.
- Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson, and J. H. Körber. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography* 16:754–763.
- Herman, T. A., and J. L. Bouzat. 2016. Range-wide phylogeography of the four-toed salamander: out of Appalachia and into the glacial aftermath. *Journal of Biogeography* 43:666–678.
- Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773–785.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society* 25:1965–1978.
- Hijmans, R. J., J. Van Etten, J. Cheng, M. Mattiuzzi, M. Sumner, J. A. Greenberg, O. P. Lamigueiro, A. Bevan, E. B. Racine, A. Shortridge, et al. 2015. raster: geographic data analysis and modeling. Version 2.4. <https://CRAN.R-project.org/package=raster>
- Hoffmann, M., C. Hilton-Taylor, A. Angulo, M. Böhm, T. M. Brooks, S. H. Butchart, K. E. Carpenter, J. Chanson, B. Collen, N. A. Cox, et al. 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330:1503–1509.
- Homan, R. N., B. S. Windmiller, and M. J. Reed. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications* 14:1547–1553.
- Hosmer, D. W., and S. Lemeshow. 1980. Goodness of fit tests for the multiple logistic regression model. *Communications in Statistics-Theory and Methods* 9:1043–1069.
- Intergovernmental Panel on Climate Change [IPCC]. 2007. *Climate change 2007: the physical science basis*. Cambridge University Press, Cambridge, United Kingdom.
- International Union for Conservation of Nature's Red List Threatened Species [IUCN]. 2020. Spatial data download. <<https://www.iucnredlist.org/resources/spatial-data-download>>. Accessed 22 Oct 2020.
- Jarnevich, C. S., and L. V. Reynolds. 2011. Challenges of predicting the potential distribution of a slow-spreading invader: a habitat suitability map for an invasive riparian tree. *Biological Invasions* 13:153–163.
- Jiménez-Valverde, A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography* 21:498–507.
- Kramer-Schadt, S., J. Niedballa, J. D. Pilgrim, B. Schröder, J. Lindenborn, V. Reinfelder, M. Stillfried, I. Heckmann, A. K. Scharf, D. M. Augeri, et al. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions* 19:1366–1379.
- Konowalik, K., and A. Nosol. 2021. Evaluation metrics and validation of presence-only species distribution models based on distributional maps with varying coverage. *Scientific Reports* 11:1–15.
- La Marca, W., J. Elith, R. S. Firth, B. P. Murphy, T. J. Regan, J. C. Woinarski, and E. Nicholson. 2019. The influence of data source and species distribution modelling method on spatial conservation priorities. *Diversity and Distributions* 25: 1060–1073.
- Lawler, J. J., S. L. Shafer, B. A. Bancroft, and A. R. Blaustein. 2010. Projected climate impacts for the amphibians of the Western Hemisphere. *Conservation Biology* 24:38–50.
- Lehtomäki, J., B. Kusumoto, T. Shiono, T. Tanaka, Y. Kubota, and A. Moilanen. 2019. Spatial conservation prioritization for the East Asian islands: a balanced representation of multitaxon biogeography in a protected area network. *Diversity and Distributions* 25:414–429.
- Lewis, J. S., M. L. Farnsworth, C. L. Burdett, D. M. Theobald, M. Gray, and R. S. Miller. 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. *Scientific Reports* 7:1–12.

- Lindenmayer, D., J. Wood, L. McBurney, C. MacGregor, K. Youngentob, and S. Banks. 2011. How to make a common species rare: a case against conservation complacency. *Biological Conservation* 144:1663–1672.
- Lobo, J. M., A. Jiménez-Valverde, and R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17:145–151.
- Malcolm, J. R., C. Liu, R. P. Neilson, L. Hansen, and L. Hannah. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* 20:538–548.
- Milanovich, J. R., W. E. Peterman, K. Barrett, and M. E. Hopton. 2012. Do species distribution models predict species richness in urban and natural green spaces? A case study using amphibians. *Landscape and Urban Planning* 107: 409–418.
- Milanovich, J. R., W. E. Peterman, N. P. Nibbelink, and J. C. Maerz. 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. *PLoS One* 5:e12189.
- Navarro-Racines, C., J. Tarapues, P. Thornton, A. Jarvis, and J. Ramirez-Villegas. 2020. High-resolution and bias-corrected CMIP5 projections for climate change impact assessments. *Scientific Data* 7:1–14.
- Ortega-Huerta, M. A., and A. T. Peterson. 2008. Modeling ecological niches and predicting geographic distributions: a test of six presence-only methods. *Revista Mexicana de Biodiversidad* 79:205–216.
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133:225–245.
- Pearce, J., and L. Venier. 2009. Are salamanders good bioindicators of sustainable forest management in boreal forests? *Canadian Journal of Forest Research* 39:169–179.
- Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361–371.
- Pecl, G. T., M. B. Araújo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I.-C. Chen, T. D. Clark, R. K. Colwell, F. Danielsen, B. Evengård, et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355:eaai9214.
- Peterson, A. T., L. P. Campbell, D. A. Moo-Llanes, B. Travi, C. González, M. C. Ferro, G. E. M. Ferreira, S. P. Brandão-Filho, E. Cupolillo, J. Ramsey, et al. 2017. Influences of climate change on the potential distribution of *Lutzomyia longipalpis* sensu lato (Psychodidae: Phlebotominae). *International Journal for Parasitology* 47:667–674.
- Peterson, A. T., M. E. Cobos, and D. Jiménez-García. 2018. Major challenges for correlational ecological niche model projections to future climate conditions. *Annals of the New York Academy of Sciences* 1429:66–77.
- Peterson, A. T., M. Papeş, and J. Soberón. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213:63–72.
- Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.
- Phillips, S. J. 2005. A brief tutorial on MaxEnt. *AT&T Research* 190:231–259.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with MaxEnt: new extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- Pineda, E., and J. M. Lobo. 2009. Assessing the accuracy of species distribution models to predict amphibian species richness patterns. *Journal of Animal Ecology* 78:182–190.
- Préau, C., A. Trochet, R. Bertrand, and F. Isselin-Nondereu. 2018. Modeling potential distributions of three European amphibian species comparing ENFA and MaxEnt. *Herpetological Conservation and Biology* 13:91–104.
- R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Radosavljevic, A., and R. P. Anderson. 2014. Making better MaxEnt models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography* 41:629–643.
- Raghavan, R. K., A. T. Peterson, M. E. Cobos, R. Ganta, and D. Foley. 2019. Current and future distribution of the lone star tick, *Amblyomma americanum* (L.) (Acari: Ixodidae) in North America. *PLoS One* 14:e0209082.
- Rebelo, H., P. Tarraso, and G. Jones. 2010. Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Global Change Biology* 16:561–576.
- Regester, K. J., K. R. Lips, and M. R. Whiles. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. *Oecologia* 147:303–314.
- Ryan, K. J., and A. J. K. Calhoun. 2014. Postbreeding habitat use of the rare, pure-diploid blue-spotted salamander (*Ambystoma laterale*). *Journal of Herpetology* 48:556–566.
- Seaborn, T., C. S. Goldberg, and E. J. Crespi. 2021. Drivers of distributions and niches of North American cold-adapted amphibians: evaluating both climate and land use. *Ecological Applications* 31:e2236.
- Searcy, C. A., and H. B. Shaffer. 2016. Do ecological niche models accurately identify climatic determinants of species ranges? *American Naturalist* 187:423–435.

- Semenov, M. A., and P. Stratonovitch. 2010. Use of multi-model ensembles from global climate models for assessment of climate change impacts. *Climate Research* 41:1–14.
- Shcheglovitova, M., and R. P. Anderson. 2013. Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. *Ecological Modelling* 269:9–17.
- Sheridan, J. A., N. M. Caruso, J. J. Apodaca, and L. J. Rissler. 2018. Shifts in frog size and phenology: testing predictions of climate change on a widespread anuran using data from prior to rapid climate warming. *Ecology and Evolution* 8: 1316–1327.
- Struecker, B. P., and J. Milanovich. 2017. Predicted suitable habitat declines for midwestern United States amphibians under future climate change and land-use change scenarios. *Herpetological Conservation and Biology* 12:635–654.
- Sutton, W. B., K. Barrett, A. T. Moody, C. S. Loftin, P. G. DeMaynadier, and P. Nanjappa. 2015. Predicted changes in climatic niche and climate refugia of conservation priority salamander species in the northeastern United States. *Forests* 6: 1–26.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285–1293.
- Swihart, R. K., T. M. Gehring, M. B. Kolozyvary, and T. E. Nupp. 2003. Responses of ‘resistant’ vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Diversity and Distributions* 9:1–18.
- Thackeray, S. J., T. H. Sparks, M. Frederiksen, S. Burthe, P. J. Bacon, J. R. Bell, M. S. Botham, T. M. Brereton, P. W. Bright, L. Carvalho, et al. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* 16:3304–3313.
- Velasco, J. A., and C. González-Salazar. 2019. Akaike information criterion should not be a “test” of geographical prediction accuracy in ecological niche modelling. *Ecological Informatics* 51:25–32.
- Veloz, S. D. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography* 36:2290–2299.
- Wake, D. B., and V. T. Vredenburg. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences* 105:11466–11473.
- Walls, S., W. Barichivich, and M. Brown. 2013. Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. *Biology* 2:399–418.
- Walton, B. M., D. Tsatisis, and M. Rivera-Sostre. 2006. Salamanders in forest-floor food webs: invertebrate species composition influences top-down effects. *Pedobiologia* 50:313–321.
- Warren, D. L., and S. N. Seifert. 2011. Ecological niche modeling in MaxEnt: the importance of model complexity and the performance of model selection criteria. *Ecological Applications* 21:335–342.
- Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters* 18:626–635.
- Zhang, V. M., D. Punzalan, and L. Rowe. 2020. Climate change has different predicted effects on the range shifts of two hybridizing ambush bug (*Phymata*, Family Reduviidae, Order Hemiptera) species. *Ecology and Evolution* 10: 12036–12048.

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