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## **SUPPLEMENTARY MATERIALS**

### **Life history and spatial traits predict extinction risk due to climate change**

Richard G. Pearson<sup>1,2</sup>, Jessica C. Stanton<sup>3</sup>, Kevin T. Shoemaker<sup>3</sup>, Matthew E. Aiello-Lammens<sup>3</sup>, Peter J. Ersts<sup>2</sup>, Ned Horning<sup>2</sup>, Damien A. Fordham<sup>4</sup>, Christopher J. Raxworthy<sup>2</sup>, Hae Yeong Ryu<sup>3</sup>, Jason McNees<sup>5</sup>, H. Reşit Akçakaya<sup>3</sup>

<sup>1</sup>Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, Gower Street, London, WC1E 6BT, UK.

<sup>2</sup>American Museum of Natural History, Central Park West at 79th Street, NY 10024, USA.

<sup>3</sup>Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794, USA.

<sup>4</sup>The Environment Institute and School of Earth & Environmental Sciences, University of Adelaide, South Australia 5005, Australia.

<sup>5</sup>NatureServe, 1101 Wilson Blvd., 15th Floor, Arlington, VA 22209, USA.

### **Supplementary Methods**

Methodological details are provided below in sections that correspond to the major steps outlined in Supplementary Fig. S4.

### **CLIMATE SCENARIOS**

The procedure for generating an annual time series of climate variables comprised three steps: First, MAGICC/SCENGEN 5.3 ([www.cgd.ucar.edu/cas/wigley/magicc](http://www.cgd.ucar.edu/cas/wigley/magicc)), a coupled gas cycle/aerosol/climate model used in the IPCC Fourth Assessment Report<sup>1</sup>, was used to generate an annual time series of future climate anomalies (2010 – 2100) using an ensemble of five atmosphere-ocean general circulation models (GCMs). Fordham *et al.*<sup>2</sup> have highlighted the advantages of working within the MAGICC/SCENGEN framework, rather than using GCM data from the Coupled Model

Intercomparison Project 3 (CMIP3) archive. GCMs were chosen according to their superior skill in reproducing seasonal precipitation and temperature across North America. Model performance was assessed following already published methods<sup>3</sup>. The five GCMs were: *UKMO-HadCM3* (UK); *CGCMA.31(T47)* (Canada); *MRI-CGCM2.3.2* (Japan); *ECHAM5/MPI-OM* (Germany); *IPSL-CM4* (France). Model terminology follows the CMIP3/AR4 multi-model data archive. Four of these models have been shown elsewhere to have good retrospective skill in reproducing recent climates at a global scale, as well as for North America<sup>2</sup>. GCM skill assessment results can be quite different depending on the variable considered, the region studied, the month or season examined, or the comparison metric used<sup>3</sup>. However, ensemble forecasts that include five or more GCMs tend to be more robust to GCM choice<sup>4</sup>.

Second, climate anomalies were downscaled to an ecologically relevant spatial resolution (~800m x 800m)<sup>5</sup>, using the “change factor” method, where the low-resolution climate signal (anomaly) from a GCM is added directly to a high-resolution baseline observed climatology (we used PRISM 1971-2000 normals<sup>6</sup>)<sup>7</sup>. Bi-linear interpolation of the GCM data (2.5 x 2.5 ° longitude/latitude) to a resolution of 0.5 x 0.5° longitude/latitude was used to reduce discontinuities in the perturbed climate at the GCM grid box boundaries<sup>2</sup>. One advantage of this method is that, by using only GCM change data, it avoids possible errors due to biases in the GCMs baseline (present-day) climate<sup>3</sup>.

Third, we generated 19 bioclimate variables<sup>8</sup> from monthly estimates of minimum temperature, maximum temperature, and mean precipitation generated by the above steps. From these 19 variables we selected 7 to use in the models based on reasoning as to the physiological/life history requirements of the species, and analysis of correlations between variables (the selected variables have relatively low correlations: maximum 0.84, mean 0.31). The 7 selected variables were: 1. Maximum Temperature of Warmest Month, 2. Minimum Temperature of Coldest Month (these two variables represent extremes of temperature, each of which is expected to have a direct physiological role in survival and reproductive success); 3. Annual Precipitation (the overall amount of precipitation each year is expected to be a good measure of suitability for amphibians and reptiles); 4. Precipitation of Driest Quarter (many amphibians and some reptiles are stressed by extended periods with little

rain, so the amount of rainfall during the driest part of the year is expected to be important); 5. Mean Temperature of Wettest Quarter (the wettest quarter is often associated with maximum amphibian and reptile activity, so temperatures during this period are likely to be important for these poikilothermic animals); 6. Temperature Seasonality (standard deviation \*100), 7. Precipitation Seasonality (Coefficient of Variation; amphibians and reptiles have the capacity to become highly specialized to local climatic conditions, especially at low latitudes, so these two measures of temperature and precipitation variability are expected to be important).

## **ECOLOGICAL NICHE MODELING**

### ***Species' occurrence data***

We obtained occurrence data from NatureServe<sup>9</sup>, which represents an international network of biological inventories, known as Natural Heritage Programs or Conservation Data Centers, in all 50 U.S. states, Canada, Latin America and the Caribbean. Most of the records come from field survey data that were georeferenced using topographic maps, imagery, or GPS units. Even for the few museum records in the data set, the localities were georeferenced by state biologists with an intimate knowledge of local geography. These data are commonly used for legal reviews and state policy making, so the accuracy is expected to be very high. NatureServe's standards and methods are extensively documented: see [www.natureserve.org/prodServices/heritagemethodology.jsp](http://www.natureserve.org/prodServices/heritagemethodology.jsp); [www.natureserve.org/prodServices/eodata.jsp](http://www.natureserve.org/prodServices/eodata.jsp). For detailed metadata concerning the specific dataset used in this study contact Jason McNees ([Jason\\_McNees@natureserve.org](mailto:Jason_McNees@natureserve.org)) or Richard Pearson ([Richard.Pearson@ucl.ac.uk](mailto:Richard.Pearson@ucl.ac.uk)). For contractual reasons that reflect the need to protect sensitive information regarding the precise location of rare, endangered, and commercially valuable species, we do not make the raw species occurrence data freely available here.

Thirty-six species of North American amphibians and reptiles were selected for inclusion in the study (Supplementary Table S1) based on the following criteria: 1. A variety of life history traits; 2. Relatively stable taxonomy; 3. >12 occurrence records (final dataset: min = 13, max = 1723, mean = 318, median = 109.5); 4. Distributions that are not close to the northern extent of the study region, to

avoid cases whereby the distribution is predicted to shift largely out of the study region under future climate. As environmental predictors, we used maps of land cover, hydrography and land surface form in addition to the climate layers described above (Supplementary Table S2).

All analyses were undertaken at the species level, based on widely accepted taxonomy as recognized by the Committee on Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico ([www.ssarherps.org/pages/comm\\_names/Index.php](http://www.ssarherps.org/pages/comm_names/Index.php)) as well as recent species descriptions (for example, the recent split of desert tortoise into *Gopherus agassizii* and *Gopherus morafka*<sup>10</sup>). Although subspecies are recognized in the NatureServe dataset, this only means that they are taxonomically valid as subspecies, not that they represent real evolutionary units. Any listed subspecies by definition is not a species. Future genetic work will either demonstrate that these are distinct species, or that they represent minor geographic variation. We therefore lumped occurrence records for subspecies to the species level.

NatureServe uses the term Element Occurrence (EO) to refer to an area of land and/or water in which a species or natural community is, or was, present. The EO's represent a great deal of processing from the underlying observation data (termed 'Source Features'), including accounting for spatial uncertainty. An EO should have practical conservation value as evidenced by potential continued (or historical) presence and/or regular recurrence at a given location. For species, the EO often corresponds with the local population, but when appropriate may be a portion of a population (e.g., long distance dispersers) or a group of nearby populations (e.g., metapopulation). Since EOs are polygons, we randomly subsampled occurrence records within EOs for use in the ecological niche models (ENMs). Eighty-eight percent of the polygons are <1km<sup>2</sup> (68% are <0.1km<sup>2</sup>), so the majority are of comparable size to our grid cell resolution; however, 12% are larger than 1km<sup>2</sup>, and there is a very small fraction (0.007%) that are >100km<sup>2</sup>. The number of occurrences that we sampled per EO was the square root of the polygon's area, with a minimum sample of 1 (for EOs <1km-sq). For each species, we randomly sampled 50 replicate datasets and ran separate ENMs for each replicate dataset. Final habitat suitability predictions represent consensus (average value per grid cell) across the 50 runs.

We deleted all records where the last observation year was pre-1990. This was necessary to avoid temporal mismatch between the occurrence records and the environmental variables that were derived from remote sensing (see below). Because of this, in some cases the distributions on which our models are based are more restricted than in IUCN assessments.

### ***Land cover***

Land cover data were obtained at 30m resolution from the MRLC National Land Cover Database ([www.mrlc.gov/](http://www.mrlc.gov/)), which is based on remotely sensed data. We use multiple years – 1992, 2001, and 2006 – and associated species' EOs with the nearest year (based on the last year of record) when running the models. For 1992, we used the retrofit product ([www.mrlc.gov/changeproduct.php](http://www.mrlc.gov/changeproduct.php)) because of incompatibility between classes between the different years. This limited us to the 8 categories of Anderson level 1. For each class, we generated a variable describing the proportion of the class within each 1km resolution cell. We did not use the MRLC Anderson Level 1 class 'open water' because this is relatively crude in comparison to the separate hydrography variables we generated, described below. Land cover for 2006 was used for all projections under future climate.

### ***Hydrography***

Given the importance of proximity to water for many of the species we studied, we characterized the availability of standing water (e.g., lakes, ponds, swamps) and moving water (e.g., streams, rivers, springs). Variables were generated using the US National Hydrography Dataset (NHD; [nhd.usgs.gov](http://nhd.usgs.gov)). The NHD was rasterized (converted from vector data to grid cells) at 25m resolution. The two variables we generated were: 1. the proportion of each 1km resolution cell that is within 200m of standing water (i.e., a lake, pond, reservoir, swamp or marsh); and 2. the proportion of each cell 1km resolution cell that is within 200m of moving water (i.e., a stream, river, area of complex channels, canal, spring or seep). Two hundred meters was selected as appropriate to represent the maximum distance a species' is likely to travel regularly to access water, based on information regarding species' home ranges and distance moved to find water.

### ***Land surface form***

Slope and aspect can be important factors for amphibians and reptiles. Reptiles tend to bask on south-facing slopes that are neither too shallow nor too steep to maximize exposure to the sun. Amphibians tend to prefer cool, moist localities on north-facing slopes. We generated two variables based on the National Elevation Dataset (<http://ned.usgs.gov>), which is derived from multiple data sources including LiDAR and SRTM. The elevation data is at 30m resolution and we applied a 5x5 low pass filter to smooth artifacts. The two variables were: (1) the proportion of each 1km resolution cell that is south-facing (SE to SW) and with a slope of 20-60 degrees; and (2) the proportion of each 1km resolution cell that is north-facing (NW to NE) and with a slope of 20-60 degrees.

### **Maxent Ecological Niche Models**

We predicted the distribution of environments suitable for species' occurrence using the maximum entropy method (Maxent)<sup>11</sup>. Maxent is a machine-learning method that characterizes ecological niches based on associations between species' occurrence records and environmental information<sup>11-14</sup>. We used a correlative rather than physiologically based species distribution model because correlative models implicitly incorporate any process, biotic and abiotic, that is statistically associated with the environmental variables and are thus less likely to overestimate the potential range<sup>15</sup>. Previous applications of mechanistic models to lizards in North America have shown overprediction of current ranges and larger range shifts under climate change than predicted by correlative models<sup>16,17</sup>, so our selection of a correlative approach is conservative. We selected a single model rather than using an 'ensemble' approach that combines multiple models<sup>18</sup> because ensemble approaches make it impractical to undertake detailed parameterization and exploration of individual models (it is preferable to apply a single method that has been carefully parameterized and for which model behavior is well understood) and because the computational demands for running even a single ENM were very high in our analyses (for each species we ran 90 annual time steps for 2 climate scenarios and each final

model was a consensus (average) from 50 replicates so as to account for uncertainty in the species occurrence data). In particular, we used Maxent because: 1. It has been shown to perform well in comparison with other methods<sup>19</sup>; 2. It requires only species' presence (not absence) data; 3. It enabled us to carefully select a regularization parameter for each species to avoid over-fitting; 4. It enabled us to explore response curves for individual variables for each species, to ensure biologically realistic models; 5. Model predictions beyond the range of training data (i.e., when extrapolating<sup>20</sup>) are constrained by clamping<sup>11</sup>, ensuring that we have a clear understanding of model behavior in these cases; 6. various graphical techniques for understanding model behavior and reliability, including the extent of extrapolation, have been developed<sup>21</sup> and are available in the free Maxent software ([www.cs.princeton.edu/~schapire/maxent](http://www.cs.princeton.edu/~schapire/maxent)).

Maxent models were calibrated using the 1971-2000 baseline climate and then projected to the annual time slices for 2010-2100. We used all seven bioclimate variables for each species since those variables were carefully selected from a larger set as being relevant for our species of interest. However, to avoid fitting models with an unnecessarily large number of variables, the most relevant land cover, hydrography, and land surface form variables were selected individually for each species based on knowledge of life history traits and demography as gleaned from the literature and expert opinion (see section Demographic Models, and Supplementary Table S2). Land cover, hydrography, and land surface form variables were kept static in the simulations, following ref.<sup>22</sup>.

The extent of the study region for selecting background points for model calibration was set for each species individually. Selection of an appropriate study region should exclude regions that the species has been unable to disperse to<sup>23</sup>. Thus, for each species we selected 10,000 background points randomly from within ecoregions that incorporate an EO (or part of an EO) for that species (i.e., background points were not selected from any ecoregion that does not include at least part of an EO). Thus, we use ecoregions to approximate the geographical bounds within which each species has had the opportunity to disperse to available environments. We used the Environmental Protection Agency's level III ecoregions of North America ([www.epa.gov/wed/pages/ecoregions/na\\_eco.htm](http://www.epa.gov/wed/pages/ecoregions/na_eco.htm)) and we used the 2006 land cover data for generating predictor variable data for the background points.

We did not implement a correction for sampling bias<sup>24</sup> on two grounds: 1. an important quality of the EO data are that individual observation points are grouped into EO's, guided by information on mobility and life history, which removes clustering due to uneven distribution of sampling effort<sup>25</sup>; and 2. the entire study region of North America has been extensively surveyed through the NatureServe network and associated data sources (e.g., museum collections).

For each species, we assessed model performance using 4-fold cross-validation for 5 (out of 50) replicate datasets. We tested regularization values of 0.5, 1, 2, and 5, and selected the regularization value that gave the highest mean AUC score across the replicates and cross-validation partitions (Supplementary Table S1).

Maxent models were run using the World Geodetic coordinate system (WGS 1984) so as to match the climate data (the MAGICC/SCENGEN method requires decimal degrees). The Maxent output grids were then projected to Albers Equal Area Conic (North America) for coupling with the population models and for all subsequent analyses.

## **BURN-IN AND ASSESSMENT PERIODS**

The occurrence locations are used to determine the initially occupied patches (as described below). However, although the study region has been extensively surveyed, occurrence data may not be complete (because site surveys may fail to find a species even though the species does use the site). Starting simulations with incomplete patch occupancy would lead to an artificial increase in simulated population sizes. To avoid this, we ran the simulations for a 10-year burn-in (or spin-up) period to let the unoccupied patches that are within dispersal distance of known occupied patches become occupied (Supplementary Fig. S5). This period begins with 1990 since that was the first year for the occurrence records (last observed occurrence must be 1990 or later, see above). We then used the next 10 years, 2000-2010, as an assessment period. All the predictor variables used in the analysis of extinction risk (i.e., random forest and boosted regression tree analyses, see below) were estimated from the simulation outputs for the assessment period. The assessment period ends and the modeled annual time slices begin with 2010 (see above). Habitat maps for the 20-year burn-in plus assessment



periods were generated by simple linear interpolation<sup>26</sup>. Since our baseline climatology is centered around 1985 (1970-2000), we ran the linear interpolation for 24 years, starting with the 1970-2000 prediction (ostensibly 1985) and ending with the predicted map for 2010.

## **LINKING HABITAT AND DEMOGRAPHY**

The potential patch structure (number, size, and spatial arrangement of patches) and its change through time for each species were specified based on the time series of habitat suitability maps (see above) using the Spatial Data module in the RAMAS GIS software package<sup>27,28</sup>. We defined a patch as the area of habitat that potentially supports one subpopulation of the modeled species. We use the term 'potential' to emphasize that even if an area may have enough contiguous suitable habitat to form a patch, it may remain unoccupied for a portion of, or the entire, duration of the simulation if it is too far from the occupied patches for the species to disperse to, or if other factors (such as demographic stochasticity) cause frequent local extinctions of the subpopulation occupying that patch. Each patch consists of a cluster of grid cells that have habitat suitability values above a threshold and that are within a neighborhood distance of each other<sup>27</sup>.

We set the habitat suitability threshold<sup>29</sup> for each species such that no more than 20% of known occurrence locations were excluded from the map of all potential patches at the first time step. Neighborhood distance, based on home range size, determines the minimum number of contiguous map cells needed to consider an area a patch. For our purposes, all species in these models had a neighborhood distance of one cell since the spatial resolution of our habitat maps were already larger than the home ranges of the species we considered. To determine which patches were occupied at the start of the simulation, we overlaid the map of all potential patches at the first time step with a map of the occurrence records buffered by a radius equal to the midpoint between the low and high values for the maximum dispersal distance ( $D_{max}$ , described below). The carrying capacity function for patches was based on the total habitat suitability (sum of the habitat suitability values for all grid cells constituting a patch). We then scaled this function such that the initial abundance for all occupied patches at the beginning of the simulation for each species was within the estimated current

abundance range. The use of ENMs to predict the upper limit of local abundance has been examined in previous studies<sup>30-33</sup>. The scaling parameter, once established for the first time step, was held constant for all subsequent time steps. Once the potential patch structure for each year was determined within a given climate scenario, we used the Habitat Dynamics module in RAMAS GIS to link this dynamic patch structure to the life history parameters of the population model (described in the next section). This method of using projected temporal changes in habitat to create metapopulation models with dynamic spatial structure has been used to model changes due to natural disturbances, succession, timber harvest<sup>34-36</sup>, as well as climate change<sup>37-41</sup>.

## **DEMOGRAPHIC MODELS**

We modeled population dynamics by drawing multiple sets of population parameters to create specific realized population models. The population parameters were sampled from a "generic life history model" (GLH model) associated with each species. Each GLH model, described below, is an age- or stage-structured, density-dependent, stochastic model designed to encompass the full set of life history parameters characteristic of a particular group of species. For each GLH model, the characteristic range of parameter values was determined based on data from the literature and was specified as a set of uniform distributions with upper and lower bounds. We developed six GLH models, for North American snakes, lizards, tortoises, turtles, small salamanders, and large salamanders.

The GLH modeling approach has two advantages. First, it avoids the need to obtain species-specific demographic parameters, which are rarely known. Second, it enables us to generalize our results concerning traits that increase risk of extinction due to climate change beyond the 36 species for which we developed ENMs. A disadvantage is that we are not able to make species-specific predictions of extinction risk, or rank these 36 species in terms their vulnerability to climate change. Therefore, our aim with the GLH models is twofold: First we estimate the average risk of extinction we expect for species with life histories similar to these six groups for which we developed GLH models.

Second, we determine the life history and spatial characteristics that make species vulnerable to extinction due to climate change.

We developed each GLH model with an age or stage structure representative of species in that group. Because species in these groups are generally polygynous with similar survival rates for males and females, shortage of males is unlikely; thus, all models are female-only (in one case with lower male than female survival, this is justified further). The number of age/stage classes ranged from 3 (for lizard GLH) to 35 (for large salamander GLH). We represented the main aspects of demography in each GLH model with 4 or 5 sets of independent parameters that were estimated as intervals. These distributional parameters included vital rates (survival rates and fecundities), temporal variability in vital rates, strengths of density dependence, dispersal rates, and spatial correlations. The lower and upper bounds of these parameters are described for each GLH in the sections below.

We used Latin hypercube sampling (LHS)<sup>42</sup> to create the specific realized population models from GLH models, and we set the number of LHS partitions to 10 times the number of independent parameters in each GLH. Thus, for each combination of species, GLH model and climate change scenario, we created 40 or 50 different specific realized population models representative of the appropriate life history strategy. To enhance our power to isolate the effects of climate change, we used the same values for demographic parameters across the two climate change scenarios and the "no climate change" scenario (i.e., we sampled and used only one set of parameters for the 3 scenarios under the same combination of species and GLH model).

Although our analysis does not allow making projections specific to any of the 36 species, each specific realized population model we randomly sample is a plausible species-specific model. Thus, although each randomly sampled model does not represent any particular species, thus we consider the ensemble of models (not any single model) we sample for each GLH model to be representative of the group of species (not any particular species) with that life history.

Temporal environmental stochasticity is incorporated by sampling annual survival rates and fecundities from random log-normal distributions. Demographic stochasticity is modeled by sampling

the annual number of survivors from a binomial distribution and number of offspring from a Poisson distribution. For further details of the demographic modeling, see ref.<sup>28</sup>.

Each specific realized population model has an explicit spatial structure (i.e., the number, size, and spatial arrangement of patches) that is based on the habitat suitability maps (see Linking habitat and demography above). Thus, in addition to within-population parameters described in the subsections below, each GLH model also includes parameters that characterize spatial relationships. These parameters relate to dispersal and the spatial (among-population) correlation of variability in survival rates and fecundity.

The following subsections detail the aspects of the six GLH models that relate demographic structure, density dependence, and variability (stochasticity). In addition to these within-population aspects, each GLH model also includes parameters that characterize spatial relationships. These parameters relate to dispersal and the spatial (among-population) correlation of variability in survival rates and fecundity.

For dispersal, we used the following function to calculate the dispersal rate ( $m$ ) from one ("source") population to another ("target") population, as a function of the distance ( $D$ , in km) from the center of the source population to the edge of the target population:

$$m = a \exp(-D/b), \text{ if } D \leq D_{\max}$$
$$m = 0, \text{ if } D > D_{\max}$$

where  $a$ ,  $b$ , and  $D_{\max}$  are model parameters described for each GLH model below.

For spatial correlation, we used the following function to calculate the correlation coefficient between the two populations as a function of the distance ( $D$ , in km) between their geographic centers:

$$\text{corr} = \exp(-D/b)$$

where  $b$  ranges from 500 to 1200 for all GLH models. These values were estimated by fitting the above function to data on the correlation of weather variables between pairs of randomly selected points in the US, and the distances between the pairs of points. The weather variables were annual maximum temperature and total annual precipitation, and were extracted from the PRISM dataset<sup>6</sup>.

The correlations were calculated based on 20 years of weather data for each location. A total of 57 locations were used, resulting in 1596 correlation values (and associated distances).

### ***Small Salamander GLH Model***

This GLH model is based on the ecology of North American small-bodied salamanders in families such as Ambystomatidae (mole salamanders) and Plethodontidae (lungless salamanders), with total body length less than about 25-30 cm. Most species in this group breed in pools of water; the larvae develop in these pools and emerge as adults to disperse in the surrounding forest. There is often a high rate of return to the same breeding pools.

#### Density dependence

Density dependence in larval stage is well documented<sup>43-47</sup>. Because the mechanism is often resource limitation, the model includes Scramble (Ricker) type density dependence. Density dependence affects fecundities only (because larval survival is incorporated into fecundity; see below). The maximum growth rate at low population size ( $R_{max}$ ) can be directly estimated from one study in which a population was monitored as it was growing from a small abundance<sup>48</sup>. In the exponential phase of this population growth, the average finite rate of increase ( $\lambda$ ) was estimated as 2.5 by fitting an exponential growth model to the first 6 years of the data.  $R_{max}$  was also estimated indirectly from a number of time series as the intercept of  $\ln(R)$  vs.  $N$  relationship, which gave  $R_{max}$  values ranging approximately from 1.1 to 4.6. Although this method may give biased estimates, applying it to a large number of time series gave a rough idea of the range of  $R_{max}$  values among species. Based on this analysis, we set the range of  $R_{max}$  values to 1.5 – 3.5.

#### Demographic structure

The model is a female-only, age-structured matrix model with 5 annual age classes, based on pre-reproductive census. Thus, fecundity is in terms of juveniles per female in the previous breeding season, and the first age class is juveniles that are almost 12 months old. Age of first reproduction is

varied between 2 and 4 years. There are species in this group that breed at 2 years<sup>49</sup>, 3 years<sup>50,51</sup>, or 4 years<sup>52</sup>. Annual survival rate is estimated as 0.6<sup>52,53</sup>. Fecundity is set to make the dominant eigenvalue of the stage matrix to be approximately 1.0, so that the stage matrix applies to a population close to its carrying capacity. The population growth rate at each time step is then determined by the density dependence relationship as described above. With this approach, fecundity is set to be between 0.667 and 1.86, depending on the age of first reproduction (see above).

### Variability

The populations of species in this group are often highly variable. Based on data in ref.<sup>52</sup> (their fig. 2 and their table 5), we estimated the coefficient of variation (CV) as 0.7 for fecundity and 0.2 for female survival rate<sup>54</sup>. When values are used in the age-structured model described above, the coefficient of variation of population size of one replicate trajectory through time is approximately 0.5, which is consistent with the median CV of population size in time series of salamanders<sup>55-57</sup>. The CV of population size in these time series ranged from approximately 0.3 to greater than 1. To represent this range of among-species variability, we used values for CV of survival ranging from 0.1 to 0.4, and CV of fecundity ranging from 0.4 to 1.4.

### Dispersal

Most individuals remain within a few hundred to 1000 m of the breeding pond<sup>58,59</sup>. However, this is mostly movement within a biological population. Dispersal between populations is based on the dispersal-distance function developed in ref.<sup>60</sup> (their fig. 3), with  $a=0.264$ ,  $b=0.35$ , and  $D_{max}=2.5\text{km}$ . To represent among-species variability, we used  $b=0.2$  and  $0.5$ , for low and high dispersal, respectively.

### ***Large Salamander GLH Model***

This GLH model describes the population demography of large-bodied salamanders, modeled after Hellbenders (*Cryptobranchus*).

### Demographic structure

Although males seem to have lower survival rate, sex ratios are often male biased. In addition, the mating system is polygynous, with several females laying eggs under the same nesting rock, to be fertilized and defended by the same male. Thus, shortage of males is unlikely, and a female-only model is justified. The model is a female-only, age-structured matrix model with 35 annual age classes, based on pre-reproductive census. Thus, fecundity is in terms of juveniles per female in the previous breeding season, and the first age class is juveniles that are almost 12 months old.

Age of first breeding is 7-8 years<sup>61</sup>. Age-specific survival rates are based on ref.<sup>62</sup> (their fig. 4) and ref.<sup>61</sup> (their fig. 3). Age-specific fecundity rates are based on data from ref.<sup>63</sup> (their fig. 3); we assume 50% of females breed, 50% of hatchlings are female (i.e., 1:1 sex ratio), and 1.7% of eggs hatch and survive the 1st year (to make  $\lambda=1$ ). The resulting stage matrix was then modified to obtain low and high values for fecundity and survival rates, in order to simulate a range of populations from declining ( $\lambda=0.9$ ) to increasing ( $\lambda=1.1$ ), at low population sizes (as described below, Ceiling model prevents a positive trend after carrying capacity is reached). The declining populations are intended to represent species, such as the Hellbender, that seem to be deterministically declining, at least in parts of their range, due to changes in habitat quality (in the case of the Hellbender, water quality and sedimentation).

### Variability

We could not find information on variability, which is typical of long-lived species. Variability in vital rates is expected to be lower than the shorter-lived small-bodied salamanders (described above). Thus, based on the small-bodied salamander generic model, we used values for CV of survival ranging from 0.05 to 0.2, and CV of fecundity ranging from 0.2 to 0.7.

### Density dependence

Males defend territories and fights between individuals, even cannibalism, are common, suggesting density dependence. However, there is no long-term census data, and most populations are declining due to habitat loss and degradation, making it impossible to estimate density dependence even if census data existed. Therefore, a simple Ceiling model<sup>27</sup> was used.

### Dispersal

Dispersal is reported to be up to 3.5 km<sup>64</sup>, suggesting longer dispersal distances than small-bodied salamanders, although a lower proportion might be dispersing<sup>63</sup>. Thus, we used  $a=0.2$ ,  $b=0.6$  to  $1.0$ , and  $D_{max}=3.5\text{km}$ .

### Density

Density estimates include 0.8–1.2 per ha<sup>65</sup> and 1-6 per ha<sup>63</sup>. Because of recent decreases in habitat quality, we based density estimates on the 2005 study. However, both of these densities were measures in the optimal habitat of streams and at a higher spatial resolution (1 ha) than the maps we are using. The density at 1-km<sup>2</sup> resolution should be much lower, even when the probability of occurrence in the 1-km<sup>2</sup> cell is close to 1.0, because only a small portion of the cell (perhaps 1%) would be the actual stream habitat. Based on this assumption, we used 1.0 km<sup>-2</sup> in cells with suitability value of 1.0.

## ***Turtle GLH Model***

### Demographic structure

Among the nine turtle species considered in this study, age to sexual maturity varied from a low of approx. 6 to 10 yrs. for the eastern box, ornate box, and bog turtles to a high of approx. 15 to 18 yrs. for the Blanding's turtle<sup>66</sup>. Therefore, we developed an age structured, female-only model with 11 age classes, including 10 pre-reproductive age classes and one composite stage class for reproductive adults. We deemed a female-only model appropriate, as most turtle species exhibit sperm storage and multiple paternity<sup>67</sup> and therefore, low male abundance is unlikely to limit reproductive output.



We parameterized the stage matrix according to pre-breeding census. Thus, fecundity was computed as the product of annual clutch size (accounting for clutch frequency), nest survival, and hatchling overwinter survival. Mean juvenile survival rates (ages 1 to 10) for freshwater turtle species vary from approximately 0.5 to 0.78<sup>68</sup>, and mean adult survival rates vary from 0.93 and 0.97<sup>69-71</sup>. We selected survival rates consistent with a turtle with 11 year age to sexual maturity (largely based on ref.<sup>72</sup>), with juvenile survival rate (age 1 to 10) of 0.75 and adult survival rate of 0.96. The model resulted in a generation time of 35 years. The model was initialized at carrying capacity. Therefore, we set the fecundity such that the dominant eigenvalue of the stage matrix was approximately 1.0, so that the stage matrix applied to a population close to its carrying capacity. The population growth rate at each time step was then determined by the density dependence relationship as described below.

#### Density dependence

Studies have indicated that nesting success may decrease with increasing population density via predator attraction to high-density nesting sites and competition for space on nesting beaches<sup>73,74</sup> (but see ref.<sup>75</sup>). Density dependence may also affect hatchling survival rate, as hatchlings and other early age classes are more vulnerable to density dependent effects such as predator search efficiency and low food availability<sup>76</sup>. We selected a scramble-type (Ricker) density dependence function which affects fecundities in a stage matrix parameterized for pre-reproductive census. Thus, fecundity is a product of annual egg production, nest survival, and hatchling survival.

To compute a range of Rmax values for the turtle GLH model, we first selected a low and high range for maximum egg production, nest survival, and hatchling survival based on a literature review for the nine turtle species considered in this study. Annual egg production for these species ranged from a low of approx. 3.5 eggs for the bog turtle<sup>77</sup> to approx. 20 eggs for the Alabama red bellied turtle<sup>78</sup>. Because we used a female-only model, we halved these numbers assuming an equal sex ratio, obtaining annual egg production values of 1.75 to 10. Studies of turtle nesting success have found that 80% to 95% of eggs hatch successfully in the absence of predation<sup>79</sup>. Nest predation rates

can be high (see section on variability below), but our model assumes that nest predation is largely density-dependent and therefore, that nest predation rates are low at low population densities.

Assuming a background nest predation rate of 10%, we set baseline maximum nest survival to 0.7 and 0.85, respectively. Maximum hatchling survival rate is likely to be at or below juvenile survival rates (0.5 to 0.78; see above); lacking more information, we set this parameter equal to juvenile survival rate for the low and high scenario. Using the above low and high estimates, we then computed maximum fecundity as the product of these three parameters (annual egg production, nest survival, and hatchling survival), yielding a range from 0.857 to 6.63. Finally, we computed  $R_{max}$  as the eigenvalue of the “low” and “high” transition matrices using this fecundity term, keeping all other transition matrix elements constant, obtaining  $R_{max}$  of 1.006 to 1.10.

### Variability

Based on ref.<sup>80</sup>, we set standard deviation of juvenile and adult survival rates as 0.015 to 0.025, for low and high values, respectively. Stochastic fluctuations in annual fecundity are likely to be much higher, but are poorly understood. Refs.<sup>72</sup> and <sup>81</sup> reported that nest survival varied from 0 to 64% with a mean of 23 to 44% annually over 27 years of rigorous surveys for Blanding’s turtles and Snapping turtles. We computed the expected standard deviation in fecundity given uniform random variation in nest survival from 0 to 64%, holding annual egg production and hatchling survival constant at “low” and “high” levels. This method yielded low and high standard deviation estimates of 0.23 and 1.44, respectively.

### Dispersal

Average dispersal distances are quite low for most freshwater turtles. In a 6-month study of Bog Turtles, 75% of all observed net displacement distances were <20m, whereas only 2% were >100m<sup>82</sup>. In about one year, radio-tracked False Map Turtles (*Graptemys pseudogeographica*) moved an average of about 0.3 to 0.4 km<sup>83</sup>. Maximum dispersal distances of 1.4 km were reported for Blanding’s Turtles<sup>84</sup>, over 3 km (over 2 years) and 3.9 km (over 4 years) were reported for Wood Turtles<sup>84</sup>, 2.7 km

for Bog Turtles<sup>82</sup>, and 4 to 5 km (over 3 years) for False Map Turtles (*Graptemys pseudogeographica*)<sup>83</sup>. Turtles displaced up to 0.8 km usually returned within days<sup>84</sup>. In a long-term mark-recapture study of a Diamondback Terrapin population (*Malaclemys terrapin*), dispersal rate (transition probabilities) between neighboring sites (separated by 0.5 to 1.0 km) varied mostly from 1% to 20%<sup>85</sup>. In Peninsula Cooter (*P. peninsularis*), average net displacement was about 0.5 km for most juveniles and adults, but 27% of males moved over 1 km<sup>84</sup>. Based on these data, we used a dispersal distance function with wide ranges for each parameter. Based on center-to-edge distances (in km), we varied maximum dispersal distance (parameter Dmax) from 1 to 3 km, average dispersal distance (parameter *b*) from 0.2 to 0.5, and maximum dispersal rate (parameter *a*) from 0.1 to 0.5.

### ***Tortoise GLH Model***

This GLH model is mostly based on the ecology of the Gopher Tortoise and Desert Tortoise.

#### Density dependence

The main mechanism of density dependence seems to be reduced growth. High densities (and often habitat destruction, i.e., a lowering of carrying capacity) lead to lower amount or quality of forage, which leads to slower growth and consequently slower maturation (e.g.,<sup>86,87</sup>). Dependence of growth on density or resource levels have been studied for other species of tortoises as well (e.g.,<sup>88</sup>).

Thus, we developed a size-structured model (see Demographic structure), parameterized for population densities at carrying capacity, in which proportion of growth to survival in each stage increases as densities decrease. In order to use this with the statistical analysis we designed, it was necessary to standardize the input by making it based only on Rmax. Thus, for a given Rmax, the program calculates MaxGroAcc, the proportion of the diagonal element in each column of the matrix (except the first) to shift to the sub-diagonal element at N=0. At each time step, the proportion transitioning to the subsequent stage is calculated as  $\text{MaxGroAcc} \cdot (1 - N/K)$ , where N and K are the population size and the carrying capacity, respectively, at that time step. Thus, when N is small, almost the entire diagonal element shifts to sub-diagonal. If N=K, none of it does. If N>K, then shift is

negative (i.e., some of the sub-diagonal element shifts to the diagonal). Because the stage matrix is unchanged when  $N=K$ , it is necessary that the stage matrix is parameterized to reflect a population at equilibrium. Thus, the stage matrix is adjusted to have an eigenvalue of 1.0. Considering the long generation time of the species, we set  $R_{max}$  from a low value of 1.05 to a high value of 1.15. The initial abundance was set equal to the carrying capacity.

### Demographic structure

The stage matrix is based on size classes and parameterized following ref.<sup>89</sup>. The generation time is about 20 years at equilibrium density (i.e., when  $N=K$ ), but changes with density. High densities lead to slower growth and consequently slower maturation (see above), increasing generation time. Conversely, lower densities lead to faster growth and shorter generation times.

### Variability

Ref.<sup>89</sup> give a range of 0.08 to 0.23 for the SD of total survival rates from a stage (i.e., transition to the next stage plus remaining in the same stage). Considering that these estimates include measurement error and spatial variability<sup>89</sup>, temporal variability is likely to account for much less than half of total observed variability. In addition, in our model, the variability for total survival is divided between variability for growth and variability for remaining in the same stage. Therefore, for SD of growth, we used a range of values from 0.005 to 0.025, except for the largest size class (which does not have a growth parameter), and the next largest size class, which has a mean value of only 0.016. For SD of the probability of remaining in the same stage, as well as for fecundity, we used a range of values from 0.015 to 0.075. This range includes the SD values used elsewhere: based on expert opinion, ref.<sup>90</sup> used standard deviations of 3.5%, 3%, 1% and 0.5%, for annual mortality of 0, 1, 2, and 3+ year age classes.

## Dispersal

Species of the genus *Gopherus* rarely move more than 2 miles from their hatching spot during their lives, though there are a few exceptions<sup>91</sup>. In *G. agassizii*, daily distance travelled ranged from 11 to 64 m, and some individuals traveled as much as 800 m in two months<sup>92</sup>. Ref.<sup>93</sup> summarized distances travelled based on several sources, with a range of 1.3 to 7.3 km over 16 days to 5 years. Dispersal distances are somewhat lower for *G. polyphemus*, with monthly distance travelled ranging from 4 to 79 m, and some individuals travelling as much as 744 m in 4 days<sup>94</sup>, and 460 m in a year<sup>91,95</sup>, and displaced individuals moving 1 to 2 km.

Based on these data, we used a dispersal distance function with wide ranges for each parameter. Based on center-to-edge distances (in km), we set the ranges for maximum dispersal distance (parameter Dmax) from 2 to 7 km, for average dispersal distance (parameter b) from 0.5 to 1.0, and for maximum dispersal rate (parameter a) from 0.1 to 0.5.

## ***Snake GLH Model***

This GLH model is based on demographic characteristics for North American snakes in the Colubridae and Viperidae families. Species in this group occupy a range of habitat types from aquatic to desert. Some in this group are ovoviviparous while some are oviparous.

## Density dependence

Although they are generally thought to be non-territorial, some species have non-overlapping home-ranges, and cannibalism is observed in some snakes<sup>96</sup>. Thus, we deemed logistic (scramble) type density dependence appropriate. This is also supported by the strong relationship between growth rate and population in time series data from ref.<sup>97</sup> (their fig 1, for two separate populations) and ref.<sup>98</sup> (their fig. 6). Based on these data, Rmax was estimated to range from 1.8 to 2.5. Although this method may sometimes give biased estimates, the consistency and strength of the relationships give confidence that this is a representative range of Rmax values. However, previous PVAs for snakes

used either no density dependence<sup>99,100</sup> or assumed a ceiling model with the carrying capacity (ceiling) based on expert opinion<sup>101</sup> and capacity of hibernacula (adults only)<sup>102,103</sup>. Because of this among-species variability, we used a relatively wide range of values for Rmax from 1.2 to 2.5.

### Demographic structure

We used a model with 4 age classes; the fourth age class was a composite age class for individuals 4 years old and older. Age of first reproduction was set at 3 years, because most snakes in this group reach maturity between 1.5-4 years of age<sup>68</sup>. Snakes generally have a 1:1 sex ratio at birth, and the mating system is polygamous, so a female-only model is appropriate. Annual survival rates vary from about 0.4 (for Green snake)<sup>104</sup> to about 0.6 (for Pacific coast garter snake)<sup>98</sup> to about 0.8 (for Eastern indigo snake)<sup>105</sup>. So, a range from 0.4 to 0.8 was used for survival, negatively correlated with a corresponding range for fecundity so as to keep the eigenvalue=1, as consistent with initial abundance being equal to carrying capacity.

### Variability

Based on ref.<sup>106</sup> (their table 3), standard deviation of annual survival rate is estimated to be 0.08. Based on ref.<sup>98</sup> (their fig. 1), the coefficient of variation of fecundity is estimated as 0.65, and the standard deviation (based on fecundity of long generation time) as 0.2. Several studies report census data, with coefficient of variation of population size ranging from 20% to 60%<sup>97,98,104,106-108</sup>. We used a range of standard deviations from 0.06 to 0.09 for survival and 0.1 to 0.3 for fecundity to obtain approximately this range of variability in size of simulated population trajectories.

### Dispersal

In Oregon Gartersnakes, juvenile males have been observed to move the longest distances (mean 73 m/mo, max 628 m/mo), adult females move the shortest (mean 11 m/mo, max 40 m/mo), and adult males and juvenile females move intermediate distances (mean 38-48 m/mo, max 321-329 m/mo)<sup>109</sup>. Other studies indicated snake populations genetically connected at distances of 7-20 km<sup>110</sup>,

potentially exchanging 1.5-2 individuals per year at a distance of about 20 km<sup>111</sup>, and dispersing at rates ranging from 0.004 to 0.3 among 3 populations that are 3-6 km apart<sup>112</sup>. Based on these data, we used a dispersal distance function, based on center-to-edge distances (in km), with maximum dispersal distance (parameter Dmax) ranging from 10 to 20 km, and average dispersal distance (parameter b) ranging from 3 to 5, and max dispersal rate (parameter a) ranging from 0.1 to 0.5.

### ***Lizard GLH Model***

This GLH model is based mostly on species in genus *Gambelia*, because the only lizard that fit our selection criteria was in this genus.

#### Density dependence

Although density dependence in genus *Gambelia* or family Crotaphytidae is not well studied, it is known that males are territorial<sup>113-116</sup>, and two instances of adult predation on hatchlings have been recorded<sup>116</sup>. In general, density dependence in lizards is well documented<sup>117-119</sup>; effects on both survival and fecundity have been noted, so our model includes effects on all stage matrix parameters. Because the mechanism is often resource limitation, the model includes Scramble (Ricker) type density dependence. The maximum growth rate at low population size (Rmax) was inferred from a study in which a population was monitored as it was growing from a small abundance<sup>116</sup>. In this study, the population growth rate was 1.4 to 2.5 depending on the time period over which it is calculated and whether juveniles are included or not.

#### Demographic structure

The model is a female-only, age-structured matrix model with 3 annual age classes, based on pre-reproductive census. Thus, fecundity is in terms of juveniles per female in the previous breeding season, and the first age class is individuals that are almost 12 months old.

Age of first reproduction is 1 year. Based on survivorship estimates of ref.<sup>116</sup>, survival rates were calculated as 0.218, 0.702, and 0.494, for 0, 1, and 2-year olds, respectively. Based on figs. 5 and 6 of

ref.<sup>116</sup>, clutch size is set at 3, 4, and 4.5 eggs for 0, 1, and 2-year olds, respectively; sex ratio is set at 50% females and proportion of females is set at 0.8. Fecundity is calculated as the product of average number of clutches per breeding female, clutch size, sex ratio, proportion breeding, and zero-year old survival rate. Average number of clutches per breeding female is set to 1.554 to make the dominant eigenvalue of the stage matrix to be approximately 1.0, so that the stage matrix applies to a population close to its carrying capacity. The population growth rate at each time step is then determined by the density dependence relationship as described above. With this approach, fecundity is set to 0.407, 0.543, 0.611 for 0, 1, and 2-year olds, respectively.

### Variability

There is only one time series (discussed above) from which variability of vital rates can be estimated. Based on this, the population growth rate ( $\lambda$ ) has a CV of about 0.5. However, this likely includes substantial measurement or sampling variability, and demographic stochasticity, as well as natural variability. We used CV of mortality and fecundity of 0.1 to 0.2 and 0.2 to 0.8, respectively. This resulted in CV of growth rate at equilibrium of 0.22 to 0.45.

### Dispersal

Most individuals in *Gambelia wislizenii* move <1 km (ref.<sup>120</sup>), but this is mostly movement within a biological population. Maximum dispersal of 2.8 km is recorded for a juvenile male<sup>120</sup>. Dispersal between populations is based on the dispersal-distance function with  $a=0.1$  to  $0.3$ ,  $b=0.2$  to  $0.5$ , and  $D_{max}=2.8$ km.

## **METAPOPULATION SIMULATIONS**

Combining each specific realized population model (sampled from a GLH model) with one of the 36 species-specific spatial structures resulted in a metapopulation model whose spatial structure changed in time as a result of changes in habitat. Each of these metapopulation models started the simulation with several occupied patches. The metapopulation size at each time step (year) was



defined as the total number of individuals in all patches at that time step. Extinction was defined as the metapopulation size reaching zero before or in the year 2100. Extinction risk for each model was calculated as the proportion of replicates (see below) going extinct.

We created two sets of population models for each spatial model: First, each of the 36 species-specific spatial structures (for each of the 3 scenarios) was modeled with the correct (matching) life history type of the species (e.g., Indigo snake matched to snake life history). Second, each species-specific spatial model was run with a randomly selected GLH model that is mis-matched from the species on which the spatial model was based (e.g., Indigo snake with tortoise life history). Our comparison of extinction risk under climate change versus under no climate change (i.e., estimated mean extinction risk of  $23\pm 7\%$  under the Policy scenario,  $28\pm 7\%$  under the Reference scenario, and  $<1$  percent without climate change; Standard Errors calculated by treating individual ENMs (species) as independent sampling units) included only the matched simulations since the aim was to estimate extinction risk for the set of species included in the study. However, both matched and mis-matched simulations were included in the subsequent analyses in which we aimed to identify variables that can predict climate-related risk (i.e., Figs. 1 and 2). Our reasoning behind including the mis-matched simulations was two-fold: 1. to minimize the influence of species as a predictor (i.e., to reduce the 'species-effect' of highly correlated or dependent variables); and 2. to enhance the coverage of life history parameter space for each unique patch structure. We explored the robustness of this reasoning by examining the effect of including versus excluding the mis-matched simulations on correlations between variables. After removing very weak correlations (Pearson  $r < 0.2$  for matched simulations), the mean difference in correlation ([absolute matched] – [absolute matched and mis-matched]) was 0.045, ranging from -0.1 to 0.3, indicating an overall reduction in correlation when mis-matched simulations are included. This finding is strengthened when considering only the 9 variables identified as most important by RF analyses: mean Pearson  $r$  reduced by 0.11 when mismatches were included. The greatest reductions in collinearity were achieved for pairs comprising a demographic and spatial variable. In many cases, scatterplots of predictor variables demonstrate that the mismatch simulations fill gaps in parameter space, likely making the resulting models more robust and

generalizable, and improving power to detect interactions between spatial and life history variables as drivers of climate-related risk (Supplementary Fig. S6).

With two GLH models (matched and mis-matched) for each of the 36 species, 3 scenarios of climate change, and 40-50 specific realized population models sampled for each of these, we ran a total of 9,720 metapopulation models, implemented in RAMAS Metapop<sup>28</sup>. Each of these models was run with 1000 replicates in order to incorporate environmental and demographic stochasticity and estimate extinction risk. Each replicate was run to simulate dynamics for 110 years, starting in 1990 and ending in 2100. Thus, a total of 1.1 billion time steps (years) were simulated. The first 20 years of each simulation comprised the burn-in period; data from this period were not used in estimating the model outputs; however, predictor variables were estimated only from this period (see below and Supplementary Fig. 5).

## **ANALYSIS OF EXTINCTION RISK DUE TO CLIMATE CHANGE**

We focused on two simulation results (response variables): 1. extinction risk; and 2. increase in extinction risk due to climate change. Extinction risk was calculated as the proportion of the 1,000 replicates that had reached a total metapopulation size of zero by the end of the simulated period. For the analysis of the importance of life history traits and spatial factors, the response variable used was the increase in extinction risk due to climate change, which was calculated as the difference in extinction risk under a climate change scenario (Policy or Reference) and under the no climate change scenario for each specific realized population model. Because we held the values selected in the LHS constant across the three scenarios (as explained above), this difference is an estimate of the increase in extinction risk that is attributable to climate change.

In the statistical analyses, we focused on increase in extinction risk due to climate change for two reasons. First, the increase due to climate change is most relevant given that our main focus is the impact of climate change. Second, our models do not incorporate other types of change (such as land-use change) because these are difficult to project and attempting to incorporate them would result in larger uncertainties. It is worth noting that the average extinction risk predicted under the no

climate change scenario is small but not zero (about 0.3% in 100 years). Thus, we believe that the results are realistic for range-restricted species that are not threatened by habitat loss and other immediate threats.

For all species, we extracted a standard set of 76 predictor variables. These variables included demographic variables, spatial variables, as well as recent trends in these variables. Demographic variables included population size, age of first reproduction, generation time, variability in survival and fecundity. Spatial variables included occupied area, number of patches (subpopulations), and various measures of connectivity and fragmentation. All of these variables were based on information from the assessment period; the demographic and spatial variables were estimated for the year 2000, and the trend variables were estimated from the simulated ten-year period 2000 to 2010 (Supplementary Fig. 5). The trend variables included trends in occupied area, population size, number of patches (subpopulations), and various measures of connectivity and fragmentation. Because the demographic structure (age vs. stage; number of age/stage classes) differed among the GLH models, we synthesized the input data on demographic structure in two main variables: generation time and the population growth rate.

As described in the main text, 21 predictor variables (Table 1) were selected from the larger set for inclusion in the statistical analysis of extinction risk. Criteria for selecting predictor variables for extinction risk (i.e., Random Forest and Boosted Regression Tree analyses) included: 1. limiting the inclusion of pairs of variables that are highly correlated; 2. ensuring that estimates of each variable could, in practice, be obtained for real species in a typical assessment situation; and 3. measurable in the present day, or based on recent trends, rather than being reliant on future predictions from models (see Main Text). Thus, we examined correlations between candidate predictor variables and in cases where two variables that are commonly used for IUCN Red List assessments were found to be strongly correlated, we selected only one of the variables. For example, we found high correlation ( $r^2=0.95$ ) between (log) occupied area and (log) extent of occurrence (range area, estimated as the area of the minimum convex polygon that includes all occupied patches), and therefore selected only one of these variables (occupied area) for inclusion in the analyses.

The extraction of predictor and response variables from the simulations, as explained above, resulted in a data table with 9,720 rows (one for each model) and columns for each response and predictor variable. We next used Random Forest (RF) and Boosted Regression Tree (BRT) analyses to assess which variables best predict extinction risk due to climate change, and how well they can predict, as explained below.

## **RANDOM FORESTS AND BOOSTED REGRESSION TREES**

Random Forests with conditional inference trees was implemented using the R package “party”<sup>121–123</sup>. For conditional inference trees, the splitting variable is the one with the strongest association (lowest p-value) with the response variable based on permutation tests. The splitting threshold is also determined based on minimizing the p-value of a non-parametric permutation test, such that the method does not make any distributional assumptions. We produced 5,000 conditional trees, each using a random subset of 50% of the data (sampled without replacement), with each split of each tree based on a different random subset of 5 variables. Our selection of the number of conditional trees and number of variables in each subset followed tests with alternative parameterizations and recommendations from the literature<sup>124</sup>. Importance of each predictor variable was determined by computing the prediction error of each tree for the out-of-bag sample (i.e., set of observations set aside for validation and not used in constructing the trees), and assessing the degree to which out-of-bag prediction error increases when the values of that predictor variable are randomly shuffled (effectively eliminating the information contributed by that predictor variable)<sup>125</sup>. The importance of a predictor variable therefore accounts for the main effects of that variable as well as its interactions with other variables. We do not present absolute values of variable importance (see Fig. 1a) because these should not be interpreted or compared over different studies<sup>125</sup>. Predictions were made by averaging across all trees in the forest.

Boosted Regression Tree models were implemented using the “gbm” and “dismo” packages in R<sup>8,126,127</sup>. In contrast to the RF algorithm, in which each tree is generated independently of other trees and predictions are performed as an average across all trees, the BRT model consists of a very large

number of trees added together in sequence, with each successive tree fit to the residuals from the previous trees in the sequence. To maximize model stability by ensuring that no single tree dominates the model, we applied a shrinkage term (learning rate) of 0.005 to each component tree. We implemented 5 splits in each component tree. As for the RF algorithm, each component tree was built using a random subset of 50% of the training data (sampled without replacement). Unlike RF, all 21 predictor variables were treated as candidates for defining the split criterion at each parent node. Also unlike RF, the split criterion was based on minimizing deviance and therefore we specified a Gaussian distribution for the residuals. All parameterizations were selected following tests and recommendations from the literature<sup>128</sup>. Importance of each predictor variable was computed simply as the total reduction in deviance associated with that variable for the full model. Like RF, this importance value accounts for main effects and high-level interactions.

We assessed model performance and predictive ability using a leave-one-out cross validation scheme in which each of the 36 species was treated in turn as an independent validation set (models were trained based on remaining 35 species). In our modeling framework, each species label corresponded to a unique time series of habitat suitability maps (derived from a Maxent model) and therefore also expressed a unique set of predictor variables measuring spatial configuration and extrinsic environmental characteristics. By using species as a data partition instead of random sampling methods (e.g., standard 10-fold cross-validation), we were able to challenge the modeling algorithm against truly independent data. Thus, the predictive performance metrics presented herein could be expected to hold for predictions of climate-related risk to additional North American species not included in this study. We used three measures of performance: AUC, root mean square error (RMSE) and deviance explained (DE). To calculate AUC, we converted extinction risk to a binary variable with a threshold of 0.5. Extinction risk had a bimodal distribution (see Supplementary Fig. S7), thus this conversion did not result in loss of information. Performance results were as follows: RF, Reference scenario: AUC = 0.86, deviance explained (DE) = 0.32, RMSE = 0.36; RF, Policy: AUC = 0.85, DE = 0.23, RMSE = 0.36; BRT, Reference: AUC = 0.80, DE = 0.18, RMSE = 0.39; BRT, Policy: AUC = 0.80, DE = 0.12, RMSE = 0.38. In contrast, using the more common approach to cross-

validation, and randomly leaving out 1/10th of models (instead of all models of a randomly selected species), [we obtain](#) AUC=0.966 (RF, Reference scenario) and AUC = 0.999 (BRT, Reference scenario).

## References

1. Intergovernmental Panel on Climate Change. *Climate Change 2007: Synthesis Report*. (2007).
2. Fordham, D. A., Wigley, T. M. L., Watts, M. J. & Brook, B. W. Strengthening forecasts of climate change impacts with multi-model ensemble averaged projections using MAGICC/SCENGEN 5.3. *Ecography* **35**, 4–8 (2012).
3. Fordham, D. A., Wigley, T. M. L. & Brook, B. W. Multi-model climate projections for biodiversity risk assessments. *Ecol. Appl.* **21**, 3317–3331 (2011).
4. Pierce, D. W., Barnett, T. P., Santer, B. D. & Gleckler, P. J. Selecting global climate models for regional climate change studies. *PNAS* **106**, 8441–8446 (2009).
5. Seo, C., Thorne, J. H., Hannah, L. & Thuiller, W. Scale effects in species distribution models: implications for conservation planning under climate change. *Biol. Lett.* **5**, 39–43 (2009).
6. PRISM Climate Group, Oregon State University. (2006). at <<http://prism.oregonstate.edu>>
7. Hulme, M., Raper, S. C. B. & Wigley, T. M. L. An integrated framework to address climate change (ESCAPE) and further developments of the global and regional climate modules (MAGICC). *Energy Policy* **23**, 347–355 (1995).
8. Hijmans, R. J., Phillips, S. J., Leathwick, J. R. & Elith, J. R package 'dismo': reference manual. (2012). at <<http://cran.r-project.org/web/packages/dismo/dismo.pdf>>
9. NatureServe. NatureServe Central Databases. (2010).
10. Murphy, R. *et al.* The dazed and confused identity of Agassiz's land tortoise, *Gopherus agassizii* (Testudines: Testudinidae) with the description of a new species and its consequences for conservation. *ZooKeys* **113**, 39 (2011).
11. Phillips, S. J., Anderson, R. P. & Schapire, R. E. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**, 231–259 (2006).

12. Merow, C., Smith, M. J. & Silander, J. A. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* no–no (2013). doi:10.1111/j.1600-0587.2013.07872.x
13. Elith, J. *et al.* A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **17**, 43–57 (2011).
14. Phillips, S. J. & Dudík, M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**, 161–175 (2008).
15. Kearney, M. & Porter, W. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **12**, 334–350 (2009).
16. Buckley, L. B. *et al.* Can mechanism inform species' distribution models? *Ecol. Lett.* **13**, 1041–1054 (2010).
17. Buckley, L. B. The range implications of lizard traits in changing environments. *Global Ecol. Biogeogr.* **19**, 452–464 (2010).
18. Araújo, M. B. & New, M. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**, 42–47 (2007).
19. Elith\*, J. *et al.* Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–151 (2006).
20. Pearson, R. G. *et al.* Model-based uncertainty in species range prediction. *J. Biogeogr.* **33**, 1704–1711 (2006).
21. Elith, J., Kearney, M. & Phillips, S. The art of modelling range-shifting species. *Methods Ecol. Evol.* **1**, 330–342 (2010).
22. Stanton, J. C., Pearson, R. G., Horning, N., Ersts, P. & Akçakaya, H. R. Combining static and dynamic variables in species distribution models under climate change. *Methods Ecol. Evol.* **3**, 349–357 (2012).
23. Anderson, R. P. & Raza, A. 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. *J. Biogeogr.* **37**, 1378–1393 (2010).

24. Phillips, S. J. *et al.* Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* **19**, 181–197 (2009).
25. Beauvais, G. P., Keinath, D. A., Hernandez, P., Master, L. & Thurston, R. Element Distribution Modeling: A Primer. (2006). at  
<[http://www.natureserve.org/prodServices/pdf/EDM\\_white\\_paper\\_2.0.pdf](http://www.natureserve.org/prodServices/pdf/EDM_white_paper_2.0.pdf)>
26. Ersts, P. J., Pearson, R. G. & Horning, N. *Grid Interpolator*. (American Museum of Natural History, Center for Biodiversity and Conservation). at  
<[http://biodiversityinformatics.amnh.org/open\\_source/gi/GridInterpolator.zip](http://biodiversityinformatics.amnh.org/open_source/gi/GridInterpolator.zip)>
27. Akçakaya, H. R. Viability analyses with habitat-based metapopulation models. *Popul. Ecol.* **42**, 45–53 (2000).
28. Akçakaya, H. R. *RAMAS GIS: Linking Landscape Data with Population Viability Analysis (version 6t)*. (Applied Biomathematics, 2012).
29. Liu, C., White, M. & Newell, G. Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* **40**, 778–789 (2013).
30. Martínez-Meyer, E., Díaz-Porrás, D., Peterson, A. T. & Yáñez-Arenas, C. Ecological niche structure and rangewide abundance patterns of species. *Biol. Lett.* **9**, (2013).
31. Tôrres, N. M. *et al.* Can species distribution modelling provide estimates of population densities? A case study with jaguars in the Neotropics. *Divers. Distrib.* **18**, 615–627 (2012).
32. VanDerWal, J., Shoo, L. P., Johnson, C. N. & Williams, S. E. Abundance and the Environmental Niche: Environmental Suitability Estimated from Niche Models Predicts the Upper Limit of Local Abundance. *Am. Nat.* **174**, 282–291 (2009).
33. Yáñez-Arenas, C., Martínez-Meyer, E., Mandujano, S. & Rojas-Soto, O. Modelling geographic patterns of population density of the white-tailed deer in central Mexico by implementing ecological niche theory. *Oikos* **121**, 2081–2089 (2012).
34. Akçakaya, H. R., Radeloff, V. C., Mladenoff, D. J. & He, H. S. Integrating landscape and metapopulation modeling approaches: viability of the sharp-tailed grouse in a dynamic landscape. *Conserv. Biol.* **18**, 526–537 (2004).



35. Akçakaya, H. R., Franklin, J., Syphard, A. D. & Stephenson, J. R. Viability of Bell's sage sparrow (*Amphispiza belli* ssp. *belli*): altered fire regimes. *Ecol. Appl.* **15**, 521–531 (2005).
36. Wintle, B. A., Bekessy, S. A., Venier, L. A., Pearce, J. L. & Chisholm, R. A. Utility of dynamic-landscape metapopulation models for sustainable forest management. *Conserv. Biol.* **19**, 1930–1943 (2005).
37. Keith, D. A. *et al.* Predicting Extinction Risks Under Climate Change: Coupling Stochastic Population Models with Dynamic Bioclimatic Habitat Models. *Biol. Lett.* **4**, 560–563 (2008).
38. Anderson, B. J. *et al.* Dynamics of range margins for metapopulations under climate change. *Proc. R. Soc. B* **276**, 1415–1420 (2009).
39. Fordham, D. A. *et al.* Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Glob. Change Biol.* **18**, 1357–1371 (2012).
40. Aiello-Lammens, M. E. *et al.* The impact of sea-level rise on Snowy Plovers in Florida: integrating geomorphological, habitat, and metapopulation models. *Glob. Change Biol.* **17**, 3644–3654 (2011).
41. Fordham, D. A. *et al.* Adapted conservation measures are required to save the Iberian lynx in a changing climate. *Nature Clim. Change* **3**, 899–903 (2013).
42. Iman, R. L. & Conover, W. J. Small sample sensitivity analysis techniques for computer models with an application to risk assessment. *Communications in Statistics - Theory and Methods* **9**, 1749–1842 (1980).
43. Wilbur, H. M. Density-dependent aspects of metamorphosis in *Ambystoma* and *Rana sylvatica*. *Ecology* **57**, 1289–1296 (1976).
44. Scott, D. E. Effects of larval density in *Ambystoma opacum*: An experiment large-scale field enclosures. *Ecology* **71**, 296–306 (1990).
45. Vanbuskirk, J. & Smith, D. C. Density-dependent population regulation in a salamander. *Ecology* **72**, 1747–1756 (1991).

46. Skelly, D. K. & Kiesecker, J. M. Venue and outcome in ecological experiments: manipulations of larval anurans. *Oikos* **94**, 198–208 (2001).
47. Vonesh, J. R. & De la Cruz, O. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia* **133**, 325–333 (2002).
48. Taylor, B. E., Scott, D. E. & Gibbons, J. W. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. *Conserv. Biol.* **20**, 792–801 (2006).
49. Palis, J. G. Breeding Migration of *Ambystoma cingulatum* in Florida. *Journal of Herpetology* **31**, 71–78 (1997).
50. Russell, A. P., Powell, G. L. & Hall, D. R. Growth and age of Alberta long-toed salamanders (*Ambystoma macrodactylum krausei*): A comparison of two methods of estimation. *Can. J. Zool.-Rev. Can. Zool.* **74**, 397–412 (1996).
51. Zambrano, L., Vega, E., Herrera, L. G., Prado, E. & Reynoso, V. H. A population matrix model and population viability analysis to predict the fate of endangered species in highly managed water systems. *Animal Conservation* **10**, 297–303 (2007).
52. Trenham, P. C., Shaffer, H. B., Koenig, W. D. & Stromberg, M. R. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* **2000**, 365–377 (2000).
53. Greenwald, K. R. Genetic data in population viability analysis: case studies with ambystomatid salamanders. *Animal Conservation* **13**, 115–122 (2010).
54. Gamble, L. R., McGarigal, K., Sigoourney, D. B. & Timm, B. C. Survival and Breeding Frequency in Marbled Salamanders (*Ambystoma opacum*): Implications for Spatio-temporal Population Dynamics. *Copeia* **2009**, 394–407 (2009).
55. Hairston Sr, N. G. in *Long-term studies of vertebrate communities* (Cody, M. L. and S.) 161–189 (Academic Press, 1996).
56. Semlitsch, R., Scott, D., Pechmann, J. & Gibbons, J. in *Long-term studies of vertebrate communities* (Cody, L. ) 217–248 (Academic Press, 1996).

57. Salvidio, S. Detecting amphibian population cycles: The importance of appropriate statistical analyses. *Biological Conservation* **142**, 455–461 (2009).
58. Faccio, S. D. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. *Journal of Herpetology* **37**, 479–489 (2003).
59. Gamble, L. R., McGarigal, K. & Compton, B. W. Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation. *Biological Conservation* **139**, 247–257 (2007).
60. Trenham, P. C., Koenig, W. D. & Shaffer, H. B. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. *Ecology* **82**, 3519–3530 (2001).
61. Peterson, C. L., Wilkinson, R. F., Topping, M. S. & Metter, D. E. Age and growth of the Ozark hellbender (*Cryptobranchus alleganiensis bishopi*). *Copeia* **1983**, 225–231 (1983).
62. Taber, C. A., Wilkinson, R. F. & Topping, M. S. Age and growth of hellbenders in the Niangua River, Missouri. *Copeia* **1975**, 633–639 (1975).
63. Peterson, C. L., Metter, D. E., Miller, B. T., Wilkinson, R. F. & Topping, M. S. Demography of the hellbender *Cryptobranchus alleganiensis* in the Ozarks. *American Midland Naturalist* **119**, 291–303 (1988).
64. Petranka, J. W. *Salamanders of the United States and Canada*. (Smithsonian Institution Press, 1998).
65. Humphries, W. J. & Pauley, T. K. Life history of the hellbender, *Cryptobranchus alleganiensis*, in a West Virginia stream. *American Midland Naturalist* **154**, 135–142 (2005).
66. Congdon, J. D. & Van Loben Sels, R. C. Relationships of reproductive traits and body size with attainment of sexual maturity and age in Blanding's turtles (*Emydoidea blandingi*). *Journal of Evolutionary Biology* **6**, 547–557 (1993).
67. Pearse, D. E. & Avise, J. C. Turtle mating systems: Behavior, sperm storage, and genetic paternity. *Journal of Heredity* **92**, 206–211 (2001).
68. Pike, D. A., Pizzatto, L., Pike, B. A. & Shine, R. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology* **89**, 607–611 (2008).

69. Iverson, J. B. Patterns of survivorship in turtles (order Testudines). *Canadian Journal of Zoology* **69**, 385–391 (1991).
70. Heppell, S. S. Application of life-history theory and population model analysis to turtle conservation. *Copeia* **1998**, 367–375 (1998).
71. Shoemaker, K. T., Breisch, A. R., Jaycox, J. W. & Gibbs, J. P. Reexamining the Minimum Viable Population Concept for Long-Lived Species. *Conservation Biology* doi:10.1111/cobi.12028
72. Congdon, J. D., Dunham, A. E. & van Loben Sels, R. Delayed Sexual Maturity and Demographics of Blanding's Turtles (*Emydoidea blandingii*): Implications for Conservation and Management of Long-Lived Organisms. *Conservation Biology* **7**, 826–833 (1993).
73. Caut, S., Hulin, V. & Girondot, M. Impact of density-dependent nest destruction on emergence success of Guianan leatherback turtles (*Dermochelys coriacea*). *Animal Conservation* **9**, 189–197 (2006).
74. Martin, T. E. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evolutionary Ecology* **2**, 37–50 (1988).
75. Burke, V. J., Rathbun, S. L., Bodie, J. R. & Gibbons, J. W. Effect of density on predation rate for turtle nests in a complex landscape. *Oikos* **83**, 3–11 (1998).
76. Fordham, D. A., Georges, A. & Brook, B. W. Indigenous harvest, exotic pig predation and local persistence of a long-lived vertebrate: managing a tropical freshwater turtle for sustainability and conservation. *Journal of Applied Ecology* **45**, 52–62 (2007).
77. Whitlock, A. L. Ecology and status of the bog turtle (*Clemmys muhlenbergii*) in New England. (2002).
78. Leary, C. *et al.* in *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. (Rhodin, A. G. J.) 019.1–019.9 (Chelonian Research Monographs, 2008).
79. Congdon, J. D., Tinkle, D. W., Breitenbach, G. L. & van Loben Sels, R. C. Nesting ecology and hatching success in the turtle *Emydoidea blandingii*. *Herpetologica* 417–429 (1983).

80. Congdon, J., Nagle, R., Kinney, O. & van Loben Sels, R. Hypotheses of aging in a long-lived vertebrate, Blanding's turtle (*Emydoidea blandingii*). *Experimental Gerontology* **36**, 813–827 (2001).
81. Congdon, J. D., Dunham, A. E. & Van Loben Sels, R. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *American Zoologist* **34**, 397–408 (1994).
82. Carter, S. L., Haas, C. A. & Mitchell, J. C. Movements and activity of bog turtles (*Clemmys muhlenbergii*) in southwestern Virginia. *Journal of Herpetology* **34**, 75–80 (2000).
83. Bodie, J. R. & Semlitsch, R. D. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia* **122**, 138–146 (2000).
84. Ernst, C. H. & Lovich, J. E. *Turtles of the united states and Canada*. (Johns Hopkins University Press, 2009).
85. Tucker, A. D., Gibbons, J. W. & Greene, J. L. Estimates of adult survival and migration for diamondback terrapins: conservation insight from local extirpation within a metapopulation. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **79**, 2199–2209 (2001).
86. Jackson Jr, C. G., Trotter, J. A., Trotter, T. H. & Trotter, M. W. Accelerated growth rate and early maturity in *Gopherus agassizi* (Reptilia: Testudines). *Herpetologica* **32**, 139–145 (1976).
87. Jackson Jr, C. G., Trotter, T. H., Trotter, J. A. & Trotter, M. W. Further observations of growth and sexual maturity in captive desert tortoises (Reptilia: Testudines). *Herpetologica* **34**, 225–227 (1978).
88. Gibson, C. W. D. & Hamilton, J. Population processes in a large herbivorous reptile: the giant tortoise of Aldabra atoll. *Oecologia* **61**, 230–240 (1984).
89. Doak, D., Kareiva, P. & Klepetka, B. Modeling population viability for the desert tortoise in the western Mojave Desert. *Ecological Applications* **4**, 446–460 (1994).
90. Miller, P. S. Preliminary population viability assessment for the gopher tortoise (*Gopherus polyphemus*) in Florida. in (Conservation Breeding Specialist Group, Apple Valley, MN., 2001).

91. Auffenberg, W. & Iverson, J. B. in *Turtles: Research and perspectives* (Morlock, H. M. an. H.) 541–569 (Wiley-Interscience, 1979).
92. Duda, J. J., Krzysik, A. J. & Freilich, J. E. Effects of drought on desert tortoise movement and activity. *Journal of Wildlife Management* **63**, 1181–1192 (1999).
93. Berry, K. H. Desert tortoise (*Gopherus agassizii*) relocation: implications of social behavior and movements. *Herpetologica* **42**, 113–125 (1986).
94. Diemer, J. E. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. *Journal of Herpetology* **26**, 158–165 (1992).
95. Epperson, D. M. & Heise, C. D. Nesting and hatchling ecology of gopher tortoises (*Gopherus polyphemus*) in southern Mississippi. *Journal of Herpetology* **37**, 315–324 (2003).
96. Breininger, D. R., Legare, M. L. & Smith, R. B. in *Species conservation and management: case studies* (Akçakaya, H. R.) 299–311 (Oxford University Press, 2004).
97. Gravel, M.-A. & Blouin-Demers, G. Long-term population estimates and synchronous variation in two populations of black rat snakes (*Elaphe obsoleta*) in Eastern Ontario. in 197–202 (Parks Research Forum of Ontario, 2006).
98. Lind, A. J., Welsh, H. H. & Tallmon, D. A. Garter snake population dynamics from a 16-year study: Considerations for ecological monitoring. *Ecological Applications* **15**, 294–303 (2005).
99. Kovács, T., Korsós, Z., Reháč, I., Corbett, K. & Miller, P. Population and Habitat Viability Assessment (PHVA) for the Hungarian Meadow Viper (*Vipera ursinii rakosiensis*). in (IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN, 2002).
100. Hyde, T., Paloski, R., Hay, R. & Miller, P. Butler's Gartersnake (*Thamnophis butleri*) in Wisconsin: Population and Habitat Viability Assessment – The Stakeholder Workshop Report. in (IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN., 2007).
101. Middleton, J. & Chu, J. Population viability analysis (PVA) of the Eastern Massasauga Rattlesnake, *Sistrurus catenatus catenatus*, in Georgian Bay Islands National Park and elsewhere in Canada. in (Parks Canada, Eastern Massasauga Rattlesnake Species Recovery Team, Gatineau, Quebec, Canada, 2004).

102. Brennan, J. M. & Tischendorf, L. *Eastern massasauga rattlesnake Sistrurus catenatus catenatus population viability in the Ojibway Prairie Complex*. (2004).
103. Brennan, J. M. & Tischendorf, L. *Population viability of the black rat snake, Elaphe obsoleta obsoleta, in the frontenac axis, ON, Canada*. (2004).
104. Plummer, M. V. Population ecology of green snakes (*Opheodrys aestivus*) revisited. *Herpetological Monographs* **11**, 102–123 (1997).
105. Hyslop, N. L., Meyers, J. M., Cooper, R. J. & Norton, T. M. Survival of radio-implanted *Drymarchon couperi* (eastern indigo snake) in relation to body size and sex. *Herpetologica* **65**, 199–206 (2009).
106. Whiting, M. J. *et al.* Population dynamics of the Concho water snake in rivers and reservoirs. *Copeia* **2008**, 438–445 (2008).
107. Weatherhead, P. J., Blouin-Demers, G. & Prior, K. A. Synchronous variation and long-term trends in two populations of black rat snakes. *Conservation Biology* **16**, 1602–1608 (2002).
108. Stevenson, D. J. *et al.* An eastern indigo snake (*Drymarchon couperi*) mark-recapture study in southeastern Georgia. *Herpetological Conservation and Biology* **4**, 30–42 (2009).
109. Welsh, H. H., Wheeler, C. A. & Lind, A. J. Spatial Ecology of the Oregon gartersnake (*Thamnophis atratus hydrophilus*) in a free-flowing stream environment. *Copeia* **2010**, 75–85 (2010).
110. Klug, P. E., Wisely, S. M. & With, K. A. Population genetic structure and landscape connectivity of the Eastern Yellowbelly Racer (*Coluber constrictor flaviventris*) in the contiguous tallgrass prairie of northeastern Kansas, USA. *Landscape Ecology* **26**, 281–294 (2011).
111. Row, J. R., Blouin-Demers, G. & Loughheed, S. C. Habitat distribution influences dispersal and fine-scale genetic population structure of eastern foxsnakes (*Mintonius gloydi*) across a fragmented landscape. *Molecular Ecology* **19**, 5157–5171 (2010).
112. Dubey, S., Brown, G. P., Madsen, T. & Shine, R. Male-biased dispersal in a tropical Australian snake (*Stegonotus cucullatus*, Colubridae). *Molecular Ecology* **17**, 3506–3514 (2008).

113. Montanucci, R. R. Observations on the San Joaquin leopard lizard, *Crotaphytus wislizenii silus* Stejneger. *Herpetologica* **21**, 270–283 (1965).
114. Tollestrup, K. Growth and reproduction in two closely related species of leopard lizards, *Gambelia silus* and *Gambelia wislizenii*. *American Midland Naturalist* **108**, 1–20 (1982).
115. Warrick, G. D., Kato, T. T. & Rose, B. R. Microhabitat use and home range characteristics of blunt-nosed leopard lizards. *Journal of Herpetology* **32**, 183–191 (1998).
116. Germano, D. J. & Williams, D. F. Population ecology of Blunt-Nosed Leopard Lizards in high elevation foothill habitat. *Journal of Herpetology* **39**, 1–18 (2005).
117. Massot, M., Clobert, J., Pilorge, T., Lecomte, J. & Barbault, R. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* **73**, 1742–1756 (1992).
118. Hasegawa, M. Density effects on life-history traits of an island lizard population. *Ecological Research* **12**, 111–118 (1997).
119. Manteuffel, V. M. & Eiblmaier, M. Density-Dependent Processes during the Juvenile Stage in the Lizard *Sceloporus virgatus*. *Journal of Herpetology* **44**, 21–27 (2010).
120. Schorr, R. A., Lambert, B. A. & Freels, E. Habitat use and home range of long-nosed leopard lizards (*Gambelia wislizenii*) in canyons of the ancients national monument, Colorado. *Herpetological Conservation and Biology* **6**, 312–323 (2011).
121. Hothorn, T., Bühlmann, P., Dudoit, S., Molinaro, A. & Laan, M. J. V. D. Survival ensembles. *Biostat* **7**, 355–373 (2006).
122. Strobl, C., Boulesteix, A.-L., Zeileis, A. & Hothorn, T. Bias in random forest variable importance measures: Illustrations, sources and a solution. *BMC Bioinformatics* **8**, 25 (2007).
123. Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T. & Zeileis, A. Conditional variable importance for random forests. *BMC Bioinformatics* **9**, 307 (2008).
124. Cutler, D. R. *et al.* Random forests for classification in ecology. *Ecology* **88**, 2783–2792 (2007).



125. Strobl, C., Malley, J. & Tutz, G. An introduction to recursive partitioning: rationale, application, and characteristics of classification and regression trees, bagging, and random forests. *Psychol. Methods* **14**, 323–348 (2009).
126. Hijmans, R. J. & Elith, J. Species Distribution Modeling with R. (2012). at <<http://cran.r-project.org/web/packages/dismo/vignettes/sdm.pdf>>
127. Ridgeway, G. Generalized Boosted Regression Models. (2013). at <<http://cran.r-project.org/web/packages/gbm/gbm.pdf>>
128. Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *J. Anim. Eco.* **77**, 802–813 (2008).