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Delaying conservation actions matters for species vulnerable to climate change

Ilona Naujokaitis-Lewis[1,2] | **Lars Y. Pomara**[1,3] | **Benjamin Zuckerberg**[1]

[1]Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin

[2]National Wildlife Research Centre, Carleton University, Environment and Climate Change Canada, Ottawa, ON, Canada

[3]Southern Research Station, USDA Forest Service, Asheville, North Carolina

Correspondence
Ilona Naujokaitis-Lewis, National Wildlife Research Centre, Carleton University, Environment and Climate Change Canada, Ottawa, ON, Canada.
Email: ilona.naujokaitis-lewis@canada.ca

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Upper Midwest and Great Lakes Landscape Conservation Cooperative; Department of Forest and Wildlife Ecology at the University of Wisconsin-Madison

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Abstract

1. Climate change vulnerability assessments are commonly used to identify species or populations at risk from global climate change, but few translate impact assessments to climate change adaptation actions. Furthermore, most climate change adaptation efforts emphasize where to implement management actions, whereas timing remains largely overlooked. The rate of modern climate change introduces urgency in evaluating whether delaying conservation actions compromises their efficacy for reaching important conservation targets.
2. We evaluated the importance of multiple climate change adaptation strategies including timing of actions on preventing extinctions for a threatened climate-sensitive species, the Eastern Massasauga rattlesnake (*Sistrurus catenatus*). We parameterized a range-wide population viability analysis model that related demographic sensitivities to drought events and human-modified land cover to assess vulnerability to future climate change. Using simulations, we assessed the efficacy and trade-offs associated with alternative climate adaptation strategies aimed at maximizing the number of future populations including when to initiate conservation actions, duration of management, number of managed populations, and local management effectiveness.
3. Population-level projections under future climate change scenarios revealed a broad-scale pattern of range contraction in the southwestern portion of the current range. Along the extinction gradient, we identified demographic strongholds and refugia critical for population persistence under climate change as well as populations at high risk of extinction and candidates for climate change adaptation actions.
4. In the context of future climate change, the timing of conservation actions was crucial; acting earlier maximized chances of achieving conservation targets. Even considering uncertainty in climate change projections, delaying actions was less efficient and introduced undesirable trade-offs including the need to implement conservation actions for longer or targeting more populations to achieve a similar conservation target.
5. *Synthesis and applications*. Our findings highlight how acting quickly reduces risk and improves outcomes for a highly vulnerable species under future climate change. Climate change vulnerability assessments require translation of

model-based outputs into tractable information for climate change adaptation planning. Quantifying trade-offs associated with the multidimensional decision space related to species conservation and recovery planning is a critical step in climate change adaptation.

KEYWORDS
climate adaptation, climate change, conservation planning, decision science, population dynamics, stage matrix model, threatened species, vulnerability assessment

1 | INTRODUCTION

During periods of rapid environmental change, conservation actions that are not implemented in a timely manner may miss windows of opportunity resulting in inefficient use of resources, or at worst, failure to reach conservation goals. Delays can occur at various points in decision-making processes for threatened species management, including listing a species (Martin et al., 2012) or delayed implementation of on-the-ground conservation measures (Martin, Camaclang, Possingham, Maguire, & Chadès, 2017). Decisions on how quickly or how long to act, or when actions should change, such as shifting resources from monitoring to alternative actions, impact strategic interventions aimed at threatened species management and ultimately biodiversity conservation (Lindenmayer, Piggott, & Wintle, 2013; Ng, McCarthy, Martin, & Possingham, 2014). Managers faced with limited resources must make these decisions in the context of other considerations such as how many sites or populations to manage, and how aggressively to manage. Improved understanding of the long-term consequences of timing of conservation actions, and of the trade-offs involved in a broader management context, can aid decision making during periods of rapid environmental change.

Anthropogenic climate change introduces both uncertainty and urgency to the timing of management actions. Climate change varies not only regionally, but across multiple ecologically relevant temporal scales (e.g., past and future changes in extremes and variability) (Garcia, Cabeza, Rahbek, & Araújo, 2014). There is increasing evidence of “tipping points” when small changes in the climate system result in strongly nonlinear responses and rapid shifts in novel climate space (Lenton, 2011). Consequently, both the rate and magnitude of exposure to climate change characterize how stressors or opportunities for adaptation vary across a species’ range over time. Even independent of the additional complexities added by synergies with land-use change (Brook, Sodhi, & Bradshaw, 2008), spatial heterogeneity and temporal nonlinearities in climate change necessitate that assessments and actions be optimized both regionally and for specific time periods.

Climate change vulnerability assessments (CCVAs) evaluate the propensity and susceptibility of multiple species to be adversely impacted by modern climate change (Pacifici et al., 2015). CCVAs incorporate a combination of intrinsic and extrinsic factors to capture sensitivity, exposure, and adaptive capacity, and link the spatial and temporal heterogeneity of future climate change to species traits or population trends (Williams, Shoo, Isaac, Hoffmann, & Langham, 2008). Population viability analysis (PVAs) is one quantitative approach used to model extinction risk under climate change and associated range shifts through the interaction between population dynamics and changes in habitat suitability over space and time (Keith et al., 2008). Although PVA models are one of the more data intensive approaches used in a CCVA context, they are amenable to integrating the important components of vulnerability: sensitivity, exposure, and adaptive capacity (e.g., McCauley, Ribic, Pomara, & Zuckerberg, 2017; Naujokaitis-Lewis et al., 2013). From a practical standpoint, these models present a powerful approach to compare alternative climate change adaptation strategies using a common (probabilistic) currency of extinction risk (Pe’er et al., 2013).

CCVAs can support decisions for managing climate-sensitive species and serve as a platform to assist with prioritization of adaptation actions. Given the resource constraints in conservation planning, quick management decisions need to be made regarding the most effective and efficient actions for reducing threats associated with future climate change (Pacifici et al., 2015). For individual species that are deemed to be especially vulnerable, translating model-based vulnerability to practical climate change adaptation strategies requires quantifying climate-demographic relationships and simulating the potential benefits of specific conservation actions (Game, Kareiva, & Possingham, 2013); however, moving from impact assessment to climate change actions is a step that still few CCVAs consider (Akçakaya, Butchart, Watson, & Pearson, 2014). Previous studies applying PVA models to evaluate alternative actions to reduce climate change impacts tend to emphasize the spatial dimensions of management such as how many populations to manage, which populations to translocate, and where and how much habitat is required to offset climate change impacts (Fordham et al., 2013; Naujokaitis-Lewis et al., 2013; Regan et al., 2012). By comparison, the consideration of the timing of conservation actions, has been less frequently assessed in PVA-based management scenarios (but see McDonald-Madden, Runge, Possingham, & Martin, 2011). PVA model outputs can include estimates of expected time to extinction and can be used to inform early warning signals of climate risk, which are relevant for listing and categorizing species at risk of extinction (Stanton, Shoemaker, Pearson, & Akçakaya, 2015). However, such metrics do not directly inform decisions related to when to start or how long to implement an action. In the context of climate change and other rapidly changing threats it is imperative to consider the timing of management actions.

The goal of our study was to develop a novel species-specific CCVA for comparing trade-offs associated with alternative adaptation strategies used for promoting persistence of a climate-sensitive species. In doing so, we evaluate a set of decision points that managers commonly face including (a) when to implement actions, (b) how long to manage, (c) how many populations to target for management actions, and (d) how aggressively to manage. We first built a range-wide PVA model that incorporates relationships between demographics and climate change for the Eastern Massasauga Rattlesnake (*Sistrurus catenatus*—hereafter EMR), a threatened species that has demonstrated rapid range contraction and vulnerability to past climate change (Pomara, LeDee, Martin, & Zuckerberg, 2014). Using our range-wide predictions of extinction risk under climate change, we explored the trade-offs associated with realistic management scenarios, while accounting for uncertainties in climate change projections. Our work addresses the heretofore overlooked issue of optimal timing of conservation actions in the context of climate change by better linking population-specific outcomes to tangible, concrete adaptation strategies that inform threatened species conservation and management into the future.

2 | MATERIALS AND METHODS

2.1 | Study area and species

EMR is found throughout the Great Lakes Region and is federally threatened in Canada (COSEWIC, 2002) and the U.S.A. (US Fish and Wildlife Service, 2016). Habitat loss is a primary driver of recent declines, and a dependency on semi-wetland habitats confers sensitivity to long-term changes in climate (Szymanski et al., 2016). Specifically, drought and flooding events pose a risk as EMR is dependent on stable water levels, especially during winter hibernation. Alongside habitat restoration and vegetation management, direct water-table manipulation is a candidate management action aimed at improving EMR persistence (Szymanski et al., 2016). We performed a CCVA for EMR by modelling range-wide population dynamics using demographic relationships linked to climate conditions and land use to assess extinction probability under different scenarios of future climate change (Figure 1). Our approach builds on the demographic models of Pomara et al. (2014), who found that historic range-wide declines in EMR were associated with demographic sensitivities to both winter drought and summer flooding.

2.2 | Environmental variables

Previous research highlights the importance of environmental drivers of EMR adult active season survival rates including winter minimum temperature, summer cumulative precipitation, anthropogenic land cover, and winter drought (Pomara et al., 2014). Winter (November-March) minimum temperature (mean temperature of the coldest month) and summer (June-August) maximum precipitation (cumulative precipitation of the wettest month) were summarized annually from 1950 to 2010 at a spatial resolution of 0.5° from the Climate Research Unit (CRU) Time-Series (TS) v.3.22 dataset (Harris, Jones, Osborn, & Lister, 2014). Our measure of anthropogenic land cover included both agricultural and urban cover classes based on

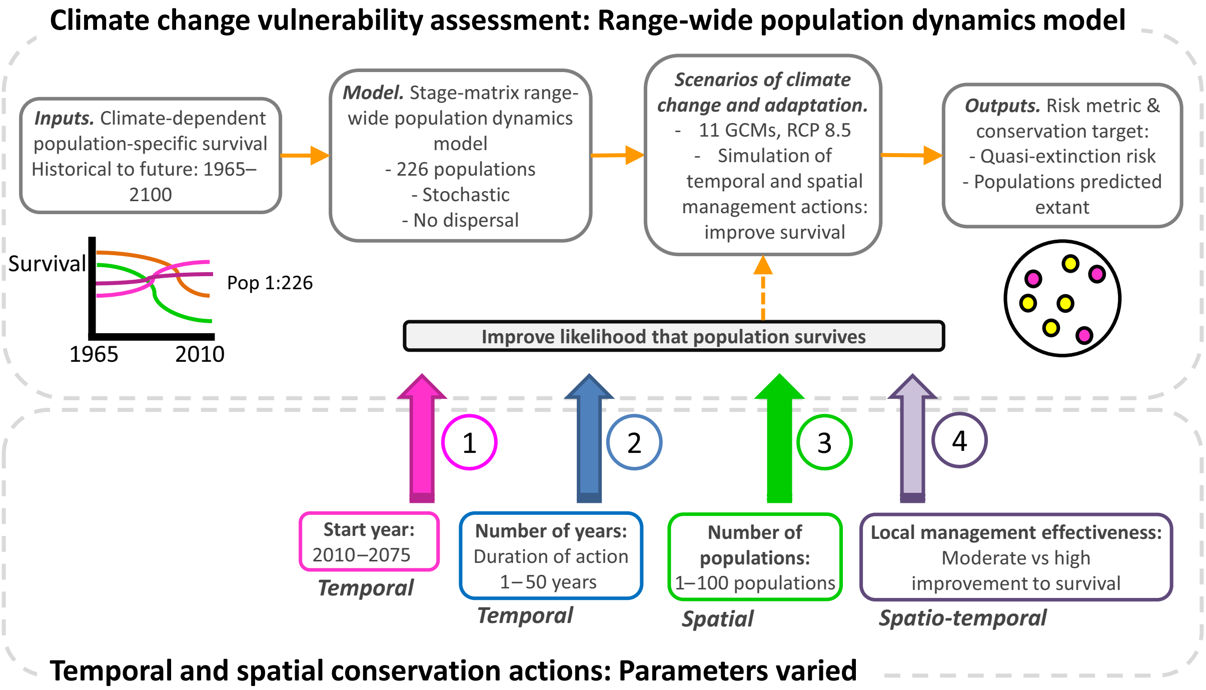

FIGURE 1 Overview of the climate change vulnerability assessment process including simulation-based approach to identify trade-offs with conservation action decision points that consider temporal dimensions: (1) when to start an action and (2) duration of action, or spatial dimensions: (3) number of populations managed and (4) local management effectiveness

the North American Land Change Monitoring System classification (NALCMS). Specifically, we used the proportion of agricultural and urban cover within a 5-km radius to capture the landscape-scale effects of human impact on land cover (NALCMS, 2010). We assumed that land cover remained static under future climate change scenarios due to unavailable future projections of land cover change.

We used the Standardised Precipitation-Evapotranspiration Index (SPEI) as a drought index instead of the Palmer-Drought Severity Index. SPEI incorporates a measure of potential evapotranspiration (PET), and by capturing the effect of changing temperatures on water availability it improves on drought indices relying only on precipitation, especially in the context of climate change applications (Vicente-Serrano, Beguería, & López-Moreno, 2010). We selected a 12-month long period for derivation of SPEI as this corresponds to a temporal resolution of drought characterization of relevance to EMR population dynamics that are modelled on an annual time-step. SPEI data were accessed from the SPEIbase v2.3.1 (Beguería, Vicente-Serrano, Reig, & Latorre, 2014), which uses climate data from the CRU TS v.3.22 dataset (Harris, Jones, et al., 2014) and employs the Penman-Monteith method for estimation of PET. Monthly SPEI values were averaged over the five winter months of November through March, for each year from 1950 to 2010, at a spatial resolution of 0.5°.

2.3 | Climate change projections

Using the delta method, we produced finer-resolution and bias corrected annual climate projections for each climate variable, including winter SPEI, winter minimum temperature, and summer cumulative precipitation. This ensured a continuous dataset from the observation-based data (recent historical climate data) and model-based climate projections (future data). Methodology followed (Harris, Grose, et al., 2014) and details are included in the Supporting Information. Gridded projections of winter minimum temperature and summer cumulative precipitation were downloaded at a resolution of 12 km (Reclamation, 2013). Gridded projections of the original SPEI data varied in spatial resolution, but were downscaled to a common resolution of 0.5° (Table S1; Cook, Smerdon, Seager, and Coats (2014)).

Global climate projections were based on the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 5 (CMIP5) multimodel dataset, for the highest Representative Concentration Pathway (RCP) 8.5. RCP8.5 corresponds to a radiative forcing of approximately 8.5 W/m^2 and represents the largest increases in greenhouse gases across all RCPs. Current emissions continue to track this high end emission scenario (Peters et al., 2013). Given the need to develop robust adaptation strategies we selected this single yet currently realistic scenario and applied a larger number of Global Circulation Models (GCMs) ($n = 11$) to capture higher inter-model climate model uncertainties (Table S1, Lutz et al., 2016).

2.4 | Survival modelling

We modelled the relationship between adult active season survival estimates and environmental variables using binomial generalized linear models with a logit link function. Survival rates from across the species range from Jones et al. (2012) were expressed as proportions, and each observation ($n = 17$) was weighted by the number of cases (i.e., telemetered snakes, which ranged from 12 to 48). Specification of main effects was constrained to a maximum of three variables to facilitate interpretation, and all variable combinations were considered using an information-theoretic approach. We used Akaike's information criterion for small sample sizes (AIC_c) to identify highest ranked models, given the data. To account for model-based uncertainty with our models of EMR active season survival, and given our primary goal of prediction, we model-averaged parameter estimates of the top 95% confidence model set (i.e., cumulative AIC_c weight of models ≤0.95) (Symonds & Moussalli, 2011). We projected active season survival rates based on model-averaged parameter estimates annually through 2100 using the adjusted future annual time series based on climate anomalies (Banner & Higgs, 2017). Thus, survival rates varied over space and time and incorporated the simulated future climate projections associated with winter minimum temperature, summer cumulative precipitation, and SPEI on an annual time-step. Projections were performed for each of the GCMs independently. Model selection, model-averaging, and assessment of variable importance were performed using the MuMIn package (Barton, 2013) using R v.3.2.0 (R Core Team, 2015).

2.5 | Climate-driven PVA model

We parameterized a population-level range-wide demographic model for EMR where fecundity and survival estimates were combined to parameterize a females-only, age-based with 11 classes, stochastic population model across the geographical distribution of EMR (Table S2, Faust, Szymanski, & Redmer, 2011; Pomara et al., 2014). Survival rates varied by population ($n_{pop} = 226$) annually from 1965 to 2100. Climate-driven population dynamics were introduced to adult (ages 3–9) and senescent (age 10) age class survivals using the statistical adult survival model projections, with future estimates (2011 onward) based on downscaled climate projections for each of the 11 GCMs independently. Using RAMAS GIS software v6.0 (Akçakaya & Root, 2013), temporal trends in adult and senescent adult survival rates were specified as time series of relative changes in survival estimates. Further details including parameterization of the climate-driven PVA model and model validation data and methods are in the Supplementary Information.

Simulations of range-wide population dynamics were initiated in 1965 and run forward to 2100, for each GCM ($n = 11$) separately. Population status from 2010 were used to initiate future model runs and were based on expert-derived data synthesized in Pomara et al. (2014; see Supplementary Information). Each simulation incorporated demographic and environmental stochasticity and was run 10,000 times. To identify populations representing demographic refugia from climate change, we quantified the projected population-level probability of quasi-extinction under climate change. We set the quasi-extinction threshold at 25 individuals following Faust et al. (2011), which reflected populations considered effectively extirpated and was based on the best available expert knowledge. We synthesized results over multiple future time points (current: 2010, mid-century: 2050, late-century: 2100) by averaging outcomes 10 years prior to minimize variation associated with annual variability in projections.

2.6 | Simulating management decision points and actions

Managers often require making decisions around number of populations to manage, the timing of management actions, and which type of management action to implement. We translated these decisions into population-level consequences using a simulation approach where investments in conservation actions were varied to explore trade-offs in the decision landscape (Figure 1). We represented these decision points by simulating improvements to adult survival given the evidence for demographic sensitivities in relation to various climatic factors (Pomara et al., 2014). For the EMR, restoring wetland habitat and direct water-table management are two different actions that might improve survival by minimizing local drought effects.

We randomly sampled the number of populations to target for management actions in a given simulation. We applied a random uniform distribution where the minimum number of populations was set to 5 with a maximum representing the number of populations with a corresponding predicted quasi-extinction probability of ≥0.1. This upper limit threshold reflects the criteria used to identify self-sustaining populations based on the recent status assessment of EMR in the USA whereby populations with a probability of persistence >0.9 were qualitatively considered robust (Szymanski et al., 2016). EMR consists of three genetically distinct subunits, where each subunit is considered to represent an area of unique adaptive diversity (Western, Central, and Eastern; Ray et al., 2013). To ensure representation across this gradient of genetic diversity, we randomly sampled populations by genetic subunit.

To address the importance of timing of conservation actions, we varied two parameters: the year that the conservation action began and the duration of management. We applied a uniform distribution to randomly sample the start year of management, which ranged from 2011 to 2090. The number of years an action was implemented varied between 1 and 50 years and was sampled from a uniform distribution. Our conservation actions were initiated during the sampled start year and implemented in successive years until the number of sampled years was reached. Our timing variables reflected when to start and how long to manage, but did not consider when to switch between alternative conservation actions.

We introduced two levels of conservation effectiveness to capture the variable effect of local (i.e., population-level) management to improve survival. Two different actions that may improve survival by minimizing local drought effects are restoring wetland habitat and direct water-table management. However, one might be more effective than the other, they might be implemented in tandem or separately, and either may be implemented with varying intensity or success. We distinguished between the two levels by modifying adult survival rates to increase to 0.78 (mean of survival estimates; *moderate level*) or to 0.90 (this represents the top 10th percentile of predicted estimates based on modelled outcomes; *high level*), when and where they fell below these rates; higher rates were not altered. This range of values represents a realistic range of survival estimates for EMR across its range (Jones et al., 2012). Once the duration of the management action ceased, the survival rates returned to the projected survival values based on the statistical demographic-environmental variables relationship.

The simulation experiments were implemented using a modified version of an R-based program that enables automated sensitivity analyses of metapopulation dynamics models using RAMAS GIS software (Naujokaitis-Lewis & Curtis, 2016). Parameters were varied simultaneously using a global sensitivity analysis approach, with a total of 2000 replications performed for each of the 11 GCMs. This resulted in a total of 22,000 replications that captured variations associated with simulations in management scenarios while addressing uncertainty associated with selection of GCM.

Population dynamics models were run to 2100 at which point population-level abundances were converted to a binary measure, whereby an extant population was defined as a population with 25 or more individuals. We chose to apply climate projections until 2100 despite the increased uncertainty with GCM projections made further into the future as quantitative analyses of probability of extinction generally require longer timeframes. This can ensure potential lagged demographic responses are captured, which can be an issue for extremely long-lived species, and this is also a standard time frame (100 years) required when using PVAs to assess IUCN Red List status (Pe'er et al., 2013). We selected the number of extant populations across the range of EMR as our metric, and our conservation goal was to maximize the projected number of extant populations at different combinations of parameter values. We used a boosted regression tree (BRT) to evaluate the relative influence of the varied parameters, including choice of GCM model, on the number of extant populations. We specified a Poisson link function and used untransformed data. We fit the BRT with up to two-way interactions by applying a tree complexity value of 2. The learning rate was specified at a value of 0.01, which was optimized to ensure a minimum of 1,000 trees were fit (Elith, Leathwick, Hastie, & Leathwick, 2008). The relative influence of each predictor variable was assessed by calculating its contribution to reducing the overall model deviance of the BRT model. We identified important modelled interactions by quantifying the strength of pairwise interactions while keeping nonfocal variables at their mean values. Implementation of the BRT model was performed in R v.3.3.0 (R Core Team, 2015) using the GBM package (Greg Ridgeway with contributions from others , 2015).

3 | RESULTS

3.1 | Demographic climate change refugia

The 6 best supported models of active season survival based on the top 95% confidence model set (i.e., cumulative AIC weight of models

≤0.95) included: winter minimum temperature (winterTemp), summer maximum precipitation (summerPrecip), winter Standardized Potential-Evapotranspiration Index (winterSPEI), and anthropogenic land cover (ALC) (Table 1). A table of the complete model selection outputs is included in Table S3. The relative variable importance values in the final model-averaged outcome across the top 95% confidence model set were 96% for winterSPEI, 88% for summerPrecip, 41% for ALC, and 22% for winterTemp (Table 2). Model projections to both mid- (2050) and late-century (2100) depicted a strong spatial gradient in quasi-extinction risk across the EMR's range with increasing risk over time (Figure 2). Quasi-extinction risk was lowest in the northeast with a distinct extinction risk gradient increasing to the southwest, highlighting a broad-scale pattern of range contraction towards the northern periphery of the range. The general spatiotemporal pattern of quasi-extinction risk was consistent across GCMs, but the largest sources of model uncertainty associated with choice of GCM occurred among populations within the south-central portion of the range, and were highest across late-century projections (Figure S1). Validation outcomes of our population dynamics model included an AUC of 0.78, indicating acceptable discrimination (Hosmer & Lemeshow, 2000). Classification metrics included a sensitivity value of 0.93, and specificity of 0.62. These outcomes indicate that the model was better at classifying true presences (extant) than absences (extirpation).

TABLE 1 Model selection outcomes of the logistic regression model of EMR active season survival as a function of winter minimum temperature (winterTemp), summer maximum precipitation (summerPrecip), winter Standardized Potential-Evapotranspiration Index (winterSPEI), and anthropogenic land cover (ALC). The table includes log likelihood (logLik), adjusted AIC for small sample sizes (AIC_c), difference from the top model (ΔAIC_c), and Akaike model weights (w_i) for the top 95% confidence model set (i.e., cumulative AIC weight of models ≤0.95) and intercept-only model

Model	logLik	AIC_c	ΔAIC_c	w_i
winterSPEI + summerPrecip	−37.59	83.03	0	0.424
winterSPEI + summerPrecip + ALC	−36.29	83.92	0.89	0.27
winterSPEI + summerPrecip + winterTemp	−37.01	85.36	2.33	0.13
ALC + winterTemp	−39.91	87.66	4.63	0.042
winterSPEI + ALC	−39.99	87.82	4.79	0.039
winterSPEI + ALC + winterTemp	−38.33	87.99	4.96	0.035
ALC	−42.17	89.20	6.17	0.019
Intercept-only	−52.04	106.35	23.32	3.7E-06

3.2 | Trade-offs between climate change adaptation decision points

Based on BRT analyses, the choice of GCM had the largest relative influence (50.4%) on the predicted number of occupied populations followed by start year of management action (24.8%), number of populations (19.2%), number of years (5%), and local management effectiveness (1.6%). Model outputs were most sensitive to the choice of GCM, with some GCMs leading to more pessimistic outcomes relative to others. Despite this disagreement among climate models, earlier implementation of management actions consistently resulted in maximising the number of predicted extant populations across the geographic range of EMR (Figure 3a, Figure S2).

We found an important interaction between start year and number of populations (Table S4, Figure 3a, Figure S2). Our results suggest that delaying implementation of management actions will require managing up to double the number of populations to achieve a similar conservation target than if actions were implemented earlier. For example, with a conservation target of 160 populations, if actions were implemented in the year 2020 approximately 40 populations would require some form of direct management, assuming a trajectory reflected by the intermediate GCM, CSIRO-MK3 (Figure 4, black-filled dot). Should actions be delayed to 2040, approximately 75 populations would require management interventions to achieve the same conservation target (Figure 4, grey-filled dot). Delaying actions by about 20 years would thus require more than double the effort (i.e., number of populations) to achieve the same conservation target should actions have been implemented earlier. Ultimately, the cost of delaying actions until 2040 is the loss of approximately six populations (i.e., a conservation target of 154 extant populations) for the same amount of effort (i.e., managing approximately 40 populations) (Figure 4, black-outlined dot). However, this lost opportunity associated with delaying actions is even greater with a higher amount of effort as demonstrated by the steep gradient space (Figure 4, grey-outlined and grey-filled dots).

We also found trade-offs between start year and the duration of management whereby delaying conservation actions would

TABLE 2 Parameter estimates, standard errors (SE), 95% confidence intervals and relative importance of model-averaged outcomes across the 95% confidence model set (cumulative $w_i \leq 0.95$) for EMR adult active season survival

Parameter	Estimate	*SE*	95% CI	Relative importance (%)
Intercept	1.246	0.138	(0.975, 1.517)	–
winterSPEI	0.447	0.194	(0.130, 0.805)	96
summerPrecip	−0.455	0.236	(−0.859, −0.178)	88
winterTemp	−0.041	0.109	(−0.508, 0.141)	22
ALC	−0.122	0.191	(−0.671, 0.079)	41

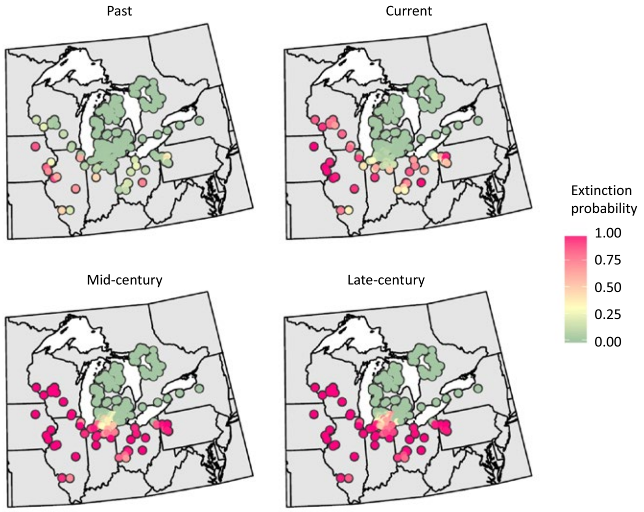

FIGURE 2 Predicted population-level extinction probability of the Eastern Massasauga Rattlesnake in the past (1980), current (2010), mid- (2050), and late-(2100) century. Future extinction predictions represent ensemble-based syntheses averaged across 11 Global Circulation Models used to project future climate change

necessitate managing for a longer number of years to achieve a similar number of predicted extant populations (Table S4, Figure 3b, Figure S3). For example, if management were to start around 2020, on average 15 years of management would be needed to reach the target of 160 extant populations (Figure 3b CSIRO-MK3). However, delaying management by just 10 years to 2030 would require more than double the number of years of active management (30–50 years) to reach the conservation target. The number of populations and duration of management was the third ranked interaction, but this combination of variables resulted in the lowest number of predicted extant populations (Table S4, Figure 3c, Figure S4). To achieve a target of approximately 160 extant populations would require implementing actions over 70 to 90 populations for a 30 to 50 year period. Although the choice of GCM was included in two interactions (with start year and number of populations respectively), the interaction size was negligible (Table S4). Overall, our results emphasize diminishing returns and loss of conservation opportunities as actions are delayed into the future.

4 | DISCUSSION

There is a critical need to develop species-specific models of climate change vulnerability and translate those model outputs into tractable information for conservation decision making. Here we demonstrate that testing alternative decision points around climate change adaptation actions through simulations can provide this linkage. Using a range-wide PVA model built on climate-demography relationships, we identified geographic regions of EMR vulnerability to future climate change and potential refugium critical for species persistence (Keppel et al., 2015). While accounting for uncertainties in future climate change projections, we illustrate the relative importance of timing of management actions in comparison to other more commonly assessed management decision points. For EMR, delaying implementation of management actions meant increased effort was needed to achieve a similar conservation target, with more lost opportunities and fewer options as delays grew longer. Our findings suggest that timing of conservation is crucial and targeted actions can buffer the effects of future climate change on range-wide persistence, but their effectiveness is mediated by interactions among different decision points and future climate uncertainty.

We documented a range-wide extirpation front that was consistent across GCMs; however, GCM selection introduced substantial variation in extinction risk (Figure S1). This variation was evident towards the contracting range edge and was most pronounced in late-century projections, an expected finding given divergence among GCM projections over time (Beaumont, Hughes, & Pitman, 2008). The resulting continuum of outcomes based on multiple individual GCMs present an envelope of possible climate futures, which would not be evident using a GCM ensemble approach (Porfirio et al., 2014). While variation across GCMs is thus evident, the disproportionate sensitivity of populations located at the contracting range edge is possibly amplified by variable population dynamics occurring along the extinction front (Anderson et al., 2009). While we incorporated potential consequences of climate change and model uncertainty associated with GCMs, our models did not account for other factors, including future land-use change. Given that land-use change is a recognized historical threat to EMR (Pomara et al., 2014), our predictions are likely conservative in this regard and underestimate predicted extinction risk as climate is the only dynamic threat considered.

Performing a CCVA and identifying populations (or species) that are most vulnerable to climate change does not automatically translate into action; managers are faced with making decisions aimed at reducing threats and improving species' recovery. Decision points can include actions that are spatial (e.g., how many and which populations to target) and temporal (e.g., when and how long to implement an action). Moving beyond impact assessment to the selection of climate change adaptation strategies that will maximize conservation outcomes is a complex process, but one that would benefit from a comparison of anticipated actions using scenario-/simulation-based approaches. In the context of CCVAs, this component remains largely over-looked (but see Fordham et al., 2013; Regan et al., 2012), especially with respect to the timing of conservation actions.

Knowing the critical management decision points, such as when it is too late to start acting, is a pervasive question for decision makers and conservation scientists. Adequate warning times for preventing extinctions will depend on a combination of factors, including political will, socio-economic considerations, species' expected responses to management actions, management objectives set for a species, and anticipated magnitude of climate change in a focal area (Akçakaya et al., 2014). We presented our results by highlighting the trade-offs associated with the multidimensional decision space. As an example, we used a conservation target of 160 extant

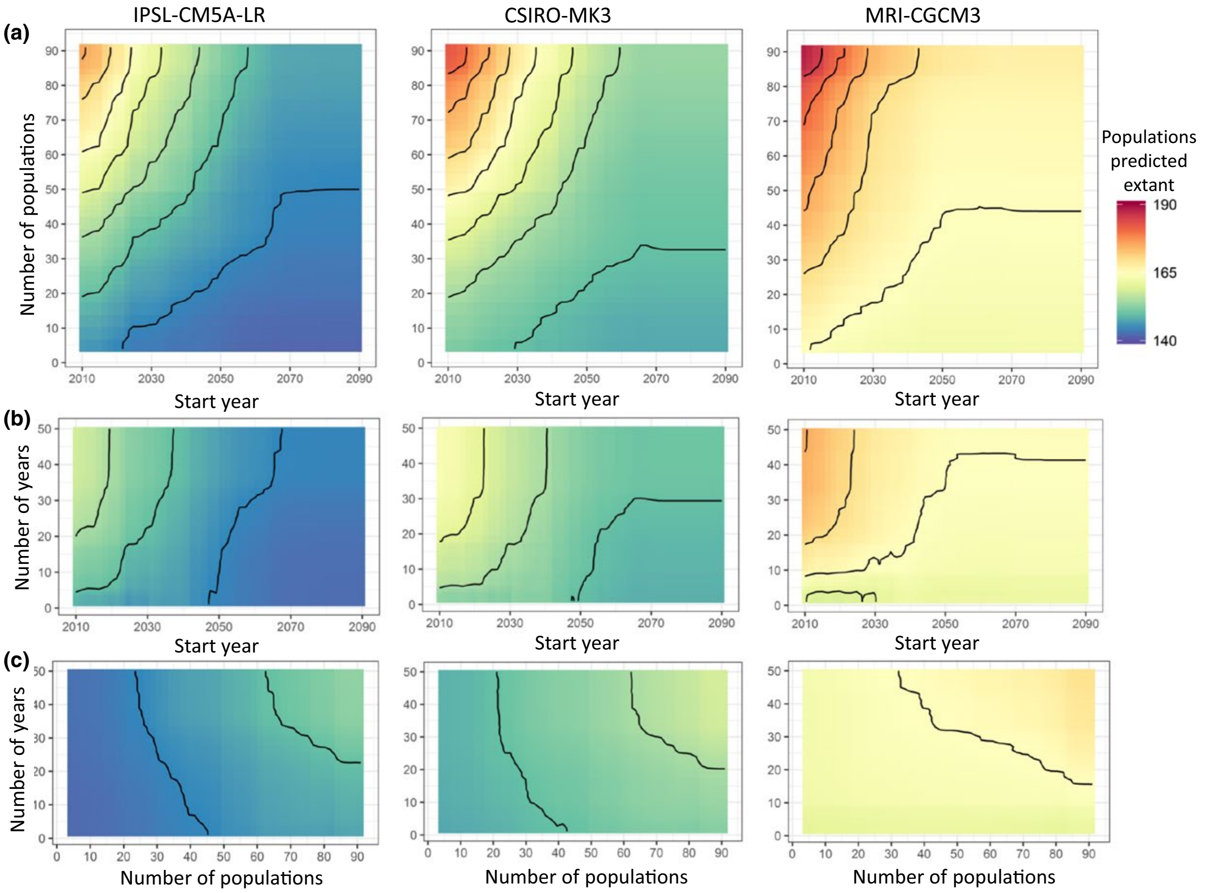

FIGURE 3 Contour plots depicting the relationship between decision points around management actions and range-wide number of populations predicted extant. Each row represents a two-way interaction based on the boosted regression tree analysis with highest ranked interactions between (a) number of populations and start year, followed by (b) number of years and start year, and (c) number of years and number of populations. Simulations were performed across 11 Global Circulation Models (GCMs), with results presented for three GCMs ranging from the worst-case scenario GCM (i.e., lowest number of predicted occupied populations; IPSL-CM5A-LR), a moderate scenario GCM (CSIRO-MK3), and the best-case scenario GCM (MRI-CGCM3). Isolines represent increments of five populations

EMR populations and highlighted the opportunity cost of delaying actions in relation to the number of populations requiring management action (Figure 3a CSIRO-MK3, Figure 4). The trade-offs are more apparent further into the future, and past the year 2045 a critical window of opportunity is surpassed as this target is no longer possible. Thus, based on these model outcomes for EMR, a critical window might be defined as the first 20 years (i.e., to 2040) as this is when consequences of trade-offs associated with conservation efforts are minimized. Because different managers may set targets differently, our approach makes the quantitative trade-offs explicit whereby informed decisions can be taken. Overall, our results suggest the advantages of early action outweigh the possible costs of delaying implementation during periods of rapid environmental change.

Managers have several different options to conserve species threatened by climate change including in situ approaches that have the potential to offset both current and impending threats (Greenwood, Mossman, Suggitt, Curtis, & Maclean, 2016). In the case of EMR, direct water-table manipulation and vegetation management are proposed in situ strategies aimed at minimizing drought and flooding effects on existing EMR populations (Faust et al., 2011). These types of habitat modifications could provide effective changes to local climatic conditions experienced by EMR and help to minimize negative outcomes associated with climate change. Managing species or populations in situ can present challenges as actions may not translate immediately into improved recovery outcomes and should also be robust to future climate change and associated uncertainties. Furthermore, knowledge associated with species' responses to a specific action is typically sparse, and different actions could result in being more or less effective for species recovery and adaptation to climate change (Bonebrake et al., 2018). While we simulated two levels of conservation effectiveness, this did not strongly influence our model outcomes. This low ranking suggests that other decision points (i.e., number of populations) be prioritized as they are expected to have a larger impact; however, there is potentially larger variability in conservation effectiveness than captured by our simulation parameters. Efforts aimed at gaining more empirical knowledge of species' responses to actions is likely to improve the effectiveness of management actions including whether there is evidence for diminishing returns of effectiveness over time.

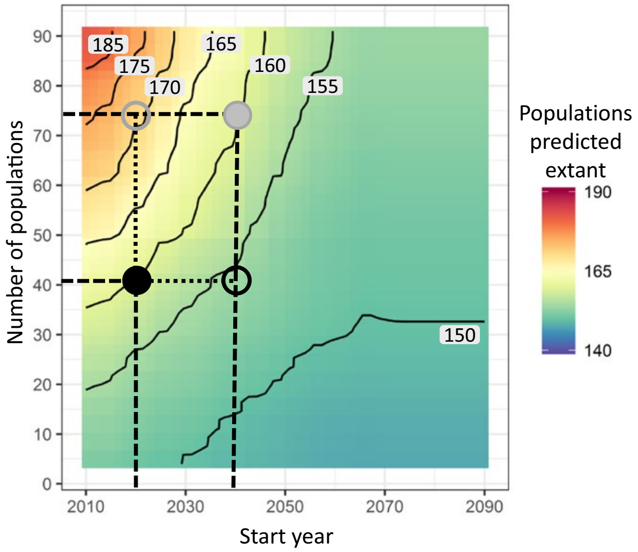

FIGURE 4 Trade-offs between decision points of number of populations to manage and start year of management actions on range-wide number of populations predicted extant for the moderate scenario GCM (CSIRO-MK3). Isolines represent increments of five populations. As an example trade-off using a conservation target of 160 populations (*z*-axis), implementing management in 2020 (*x*-axis) at 40 populations (*y*-axis) depicts the advantages of acting quickly (black-filled dot) and is contrasted by consequences of delaying actions to 2040 which would require management of 75 populations to achieve the same target (grey-filled dot). The black-outlined dot represents the lowered expected conservation target (154 predicted populations extant) if the number of populations managed remained constant (40) but the start year of management was delayed. The difference between the grey-filled and grey-outlined dot is the (greater) lost opportunity associated with delaying actions at higher level of number of populations managed

Deciding how to incorporate climate model uncertainties into decision-making will depend on management context and levels of acceptable risk tolerance. Relative to decision points around conservation actions, the choice of GCM had the largest influence on the predicted number of occupied populations under future climate change. While this resulted in different quantitative predictions across GCMs resulting in a range of outcomes from worst-case scenarios to best case ones, the patterns and trade-offs between different conservation strategies remained consistent across GCMs. Despite this consistency, our projections of extinction risk are likely more optimistic owing to a higher false positive rate, based on our model validation, where future extirpations may have been misclassified as persistence. While our projections further into the future remained more uncertain, further research and subsequent model refinement as new information becomes available have an important role to play in reducing uncertainties and informing robust actions (Shoo et al., 2013). More risk-averse management may be appropriate for populations showing higher disagreement among GCMs, as management outcomes are less certain.

Identifying trade-offs associated with alternative conservation actions requires several simplifying assumptions in our simulations. We simulated actions that improved active season survival rates, assuming that implementation translated to an immediate increase in survival rates. Additionally, once the duration of an action was complete, survival rates returned to the original projections rather than staying elevated. Depending on the specific management action, population-level responses could lag behind initial implementation. For example, direct water-table manipulation may result in immediate effects on survival while attempting to improve water-table levels indirectly through restoration of vegetation is more likely to produce a more lagged (i.e., slower) response at the population level. This assumption may have resulted in overly optimistic results, but reinforces the need to act quickly. While our approach assists in prioritizing and evaluating temporal relative to spatial dimensions of conservation actions, we did not explicitly consider costs and subsequent trade-offs in a cost-efficiency framework (Sebastián-González et al., 2011), nor when to shift between management actions, which are important next steps. Despite these limitations, our approach to simulating both climate-driven threats and the effectiveness of adaptation actions in a single framework can be readily extended to other species and systems, which include species currently known to be climate-sensitive and those anticipated to be most vulnerable to future climate change.

Real-world situations where decisions have been delayed have clearly contributed to species extinctions (Martin et al., 2012). These delays in conservation action have even greater implications during a time of rapid climate change that is unprecedented over decades and millennia (IPCC, 2014). Conservation prioritizations for climate-threatened species have largely not addressed timing of conservation, yet we show here that timing is critical for improving persistence of a climate-threatened species, even while accounting for uncertainties of future climate change. Delays in decisions and actions on-the-ground are likely to have significant negative impacts on both currently declining climate-sensitive species and those vulnerable to unprecedented changes in climate and land-use practices. There is an urgent need to make decisions related to the management of climate-sensitive species while there is still an opportunity to act.

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AUTHORS' CONTRIBUTIONS

I.N.-L. conceived the study and designed the methodology; I.N.-L. and L.P. collected the data. I.N.-L. analysed the data; I.N.-L. led the writing of the manuscript. All authors (I.N.-L., L.P., and B.Z.)

contributed critically to the manuscript and all authors gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.nn2j150 (Naujokaitis-Lewis, Pomara, & Zuckerberg, 2018).

Note: Eastern Massasauga Rattlesnake population status and location data are sensitive and have not been archived.

ORCID

Ilona Naujokaitis-Lewis http://orcid.org/0000-0001-9504-4484

REFERENCES

Akçakaya, H. R., Butchart, S. H. M., Watson, J. E. M., & Pearson, R. G. (2014). Preventing species extinctions resulting from climate change. *Nature Climate Change*, *4*(12), 1048–1049. https://doi.org/10.1038/nclimate2455

Akçakaya, H. R., & Root, W. T. (2013). *RAMAS GIS: Linking spatial data with population viability analysis (version 6.0)*. Setauket, NY: Applied Biomathematics.

Anderson, B. J., Akcakaya, H. R., Araujo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W., & Brook, B. W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1661), 1415–1420. https://doi.org/10.1098/rspb.2008.1681

Banner, K. M., & Higgs, M. D. (2017). Considerations for assessing model averaging of regression coefficients. *Ecological Applications*, *27*(1), 78–93. https://doi.org/10.1002/eap.1419

Barton, K. (2013). MuMIn: Multi-model inference. R package version 1.9.13. Retrieved from http://CRAN.R-project.org/package=MuMIn

Beaumont, L. J., Hughes, L., & Pitman, A. J. (2008). Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters*, *11*(11), 1135–1146. https://doi.org/10.1111/j.1461-0248.2008.01231.x

Beguería, S., Vicente-Serrano, S. M., Reig, F., & Latorre, B. (2014). Standardized precipitation evapotranspiration index (SPEI) revisited: Parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *International Journal of Climatology*, *34*, 3001–3023. https://doi.org/10.1002/joc.3887

Bonebrake, T. C., Brown, C. J., Bell, J. D., Blanchard, J. L., Chauvenet, A., Champion, C., … Pecl, G. T. (2018). Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. *Biological Reviews*, *93*(1), 284–305. https://doi.org/10.1111/brv.12344

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. (2008). Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, *23*(8), 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Cook, B. I., Smerdon, J. E., Seager, R., & Coats, S. (2014). Global warming and 21st century drying. *Climate Dynamics*, *43*, 2607–2627. https://doi.org/10.1007/s00382-014-2075-y

COSEWIC. (2002). *COSEWIC assessment and update status report on the massasauga* Sistrurus catenatus *in Canada*. Ottawa, ON: Committee on the Status of Endangered Wildlife in Canada.

Elith, J., Leathwick, J. R., Hastie, T., & Leathwick, J. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*(4), 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Faust, L., Szymanski, J., & Redmer, M. (2011). *Range wide extinction risk modeling for the Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*)*. Chicago, IL: Lincoln Park Zoo and U.S. Fish and Wildlife Service.

Fordham, D. A., Akçakaya, H. R., Brook, B. W., Rodríguez, A., Alves, P. C., Civantos, E., … Araújo, M. B. (2013). Adapted conservation measures are required to save the Iberian lynx in a changing climate. *Nature Climate Change*, *3*(10), 899–903. https://doi.org/10.1038/nclimate1954

Game, E. T., Kareiva, P., & Possingham, H. P. (2013). Six common mistakes in conservation priority setting. *Conservation Biology*, *27*(3), 480–485. https://doi.org/10.1111/cobi.12051

Garcia, R., Cabeza, M., Rahbek, C., & Araújo, M. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, *344*(6183), 1247579. https://doi.org/10.1126/science.1247579

Greenwood, O., Mossman, H. L., Suggitt, A. J., Curtis, R. J., & Maclean, I. M. D. (2016). Using in situ management to conserve biodiversity under climate change. *Journal of Applied Ecology*, *53*, 885–894. https://doi.org/10.1111/1365-2664.12602

Greg Ridgeway with Contributions from Others (2015). gbm: Generalized boosted regression models. R package version 2.1.2. https://CRAN.R-project.org/package=gbm

Harris, R. M. B., Grose, M. R., Lee, G., Bindoff, N. L., Porfirio, L. L., & Fox-Hughes, P. (2014). Climate projections for ecologists. *Wiley Interdisciplinary Reviews: Climate Change*, *5*(5), 621–637. https://doi.org/10.1002/wcc.291

Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations – The CRU TS3.10 Dataset. *International Journal of Climatology*, *34*(3), 623–642. https://doi.org/10.1002/joc.3711

Hosmer, D. W., & Lemeshow, S. (2000). *Applied logistic regression* (2nd ed.). New York, NY: John Wiley & Sons Inc. https://doi.org/10.1002/0471722146

IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland.

Jones, P. C., King, R. B., Bailey, R. L., Bieser, N. D., Bissell, K., Campa, H., … Yagi, A. (2012). Range-wide analysis of eastern massasauga survivorship. *Journal of Wildlife Management*, *76*(8), 1576–1586. https://doi.org/10.1002/jwmg.418

Keith, D., Akçakaya, H. R., Thuiller, W., Midgley, G. F., Pearson, R. G., Phillips, S. J., … Rebelo, T. G. (2008). Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, *4*(5), 560–563. https://doi.org/10.1098/rsbl.2008.0049

Keppel, G., Mokany, K., Wardell-Johnson, G., Phillips, B., Welbergen, J., & Reside, A. (2015). The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment*, *3*, 106–112. https://doi.org/10.1890/140055

Lenton, T. (2011). Early warning of tipping points. *Nature Climate Change*, *1*(4), 201–209. https://doi.org/10.1038/nclimate1143

Lindenmayer, D. B., Piggott, M. P., & Wintle, B. A. (2013). Counting the books while the library burns: Why conservation monitoring programs need a plan for action. *Frontiers in Ecology and the Environment*, *11*(10), 549–555. https://doi.org/10.1890/120220

Lutz, A. F., ter Maat, H. W., Biemans, H., Shrestha, A. B., Wester, P., & Immerzeel, W. W. (2016). Selecting representative climate models for climate change impact studies: An advanced envelope-based selection approach. *International Journal of Climatology*, *36*(12), 3988–4005. https://doi.org/10.1002/joc.4608

Martin, T. G., Camaclang, A. E., Possingham, H. P., Maguire, L. A., & Chadès, I. (2017). Timing of protection of critical habitat matters. *Conservation Letters*, *10*(3), 308–316. https://doi.org/10.1111/conl.12266

Martin, T. G., Nally, S., Burbidge, A. A., Arnall, S., Garnett, S. T., Hayward, M. W., … Possingham, H. P. (2012). Acting fast helps avoid extinction. *Conservation Letters*, *5*(4), 274–280. https://doi.org/10.1111/j.1755-263X.2012.00239.x

McCauley, L. A., Ribic, C. A., Pomara, L. Y., & Zuckerberg, B. (2017). The future demographic niche of a declining grassland bird fails to shift poleward in response to climate change. *Landscape Ecology*, *32*(4), 807–821. https://doi.org/10.1007/s10980-017-0487-x

McDonald-Madden, E., Runge, M. C., Possingham, H. P., & Martin, T. G. (2011). Optimal timing for managed relocation of species faced with climate change. *Nature Climate Change*, *1*(5), 261–265. https://doi.org/10.1038/nclimate1170

NALCMS. (2010). *2005 North American land cover at 250 m spatial resolution*. Produced by Natural Resources Canada/Canadian Center for Remote Sensing (NRCan/CCRS), United States Geological Survey (USGS); Insituto Nacional de Estad ıstica y Geograf ıa (INEGI), Comisi on Nac.

Naujokaitis-Lewis, I., & Curtis, J. M. R. (2016). Advances in global sensitivity analyses of demographic-based species distribution models to address uncertainties in dynamic landscapes. *PeerJ*, *4*, e2204. https://doi.org/10.7717/peerj.2204

Naujokaitis-Lewis, I., Curtis, J. M. R., Tischendorf, L., Badzinski, D., Lindsay, K., & Fortin, M.-J. (2013). Uncertainties in coupled species distribution–metapopulation dynamics models for risk assessments under climate change. *Diversity and Distributions*, *19*(5–6), 541–554. https://doi.org/10.1111/ddi.12063

Naujokaitis-Lewis, I., Pomara, L., & Zuckerberg, B. Z. (2018). Data from: Delaying conservation actions matters for species vulnerable to climate change. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.nn2j150

Ng, C. F., McCarthy, M. A., Martin, T. G., & Possingham, H. P. (2014). Determining when to change course in management actions. *Conservation Biology*, *28*(6), 1617–1625. https://doi.org/10.1111/cobi.12382

Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., … Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, *5*(3), 215–224. https://doi.org/10.1038/nclimate2448

Pe'er, G., Matsinos, Y. G., Johst, K., Franz, K. W., Turlure, C., Radchuk, V., … Henle, K. (2013). A protocol for better design, application, and communication of population viability analyses. *Conservation Biology*, *27*(4), 644–656. https://doi.org/10.1111/cobi.12076

Peters, G. P., Andrew, R. M., Boden, T., Canadell, J. G., Ciais, P., Le Quéré, C., … Wilson, C. (2013). The challenge to keep global warming below 2°C. *Nature Climate Change*, *3*(1), 4–6. https://doi.org/10.1038/nclimate1783

Pomara, L. Y., LeDee, O. E., Martin, K. J., & Zuckerberg, B. (2014). Demographic consequences of climate change and land cover help explain a history of extirpations and range contraction in a declining snake species. *Global Change Biology*, *20*(7), 2087–2099. https://doi.org/10.1111/gcb.12510

Porfirio, L. L., Harris, R. M. B., Lefroy, E. C., Hugh, S., Gould, S. F., Lee, G., … Mackey, B. (2014). Improving the use of species distribution models in conservation planning and management under climate change. *PLoS ONE*, *9*(11), e113749. https://doi.org/10.1371/journal.pone.0113749

R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ray, J. W., King, R. B., Duvall, M. R., Robinson, J. W., Jaeger, C. P., Dreslik, M. J., … Mulkerin, D. (2013). Genetic analysis and captive breeding program design for the eastern massasauga *Sistrurus catenatus catenatus*. *Journal of Fish & Wildlife Management*, *4*, 104–113. https://doi.org/10.3996/032012-JFWM-026

Reclamation. (2013). *Downscaled CMIP3 and CMIP5 climate and hydrology projections: Release of downscaled CMIP5 climate projections, comparison with preceding information, and summary of user needs*. Denver, CO: Reclamation.

Regan, H. M., Syphard, A. D., Franklin, J., Swab, R. M., Markovchick, L., Flint, A. L., … Zedler, P. H. (2012). Evaluation of assisted colonization strategies under global change for a rare, fire-dependent plant. *Global Change Biology*, *18*(3), 936–947. https://doi.org/10.1111/j.1365-2486.2011.02586.x

Sebastián-González, E., Sánchez-Zapata, J. A., Botella, F., Figuerola, J., Hiraldo, F., & Wintle, B. (2011). Linking cost efficiency evaluation with population viability analysis to prioritize wetland bird conservation actions. *Biological Conservation*, *144*(9), 2354–2361. https://doi.org/10.1016/j.biocon.2011.06.015

Shoo, L. P., Hoffmann, A., Garnett, S., Pressey, R., Williams, Y., Taylor, M., … Williams, S. (2013). Making decisions to conserve species under climate change. *Climatic Change*, *119*, 239–246. https://doi.org/10.1007/s10584-013-0699-2

Stanton, J., Shoemaker, K., Pearson, R., & Akçakaya, H. (2015). Warning times for species extinctions due to climate change. *Global Change Biology*, *21*(3), 1066–1077. https://doi.org/10.1111/gcb.12721

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*(1), 13–21. https://doi.org/10.1007/s00265-010-1037-6

Szymanski, J., Pollack, C., Ragan, L., Redmer, M., Clemency, L., Voorhies, K., & Jaka, J. (2016). Species status assessment for the Eastern Massasauga Rattlesnake (Sistrurus catenatus). Retrieved from https://www.fws.gov/midwest/endangered/reptiles/eama/pdf/SSAFinalV2July2016EMR.pdf

US Fish and Wildlife Service. (2016). Endangered and threatened wildlife and plants; threatened species status for the Eastern Massasauga Rattlesnake (*Sistrurus catenatus*); Final Rule. *Federal Register*, *81*, 67193–67214.

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate*, *23*(7), 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*, *6*(12), 2621–2626. https://doi.org/e32510.1371/journal.pbio.0060325

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