



Climate change and collapsing thermal niches of desert reptiles and amphibians: Assisted migration and acclimation rescue from extirpation

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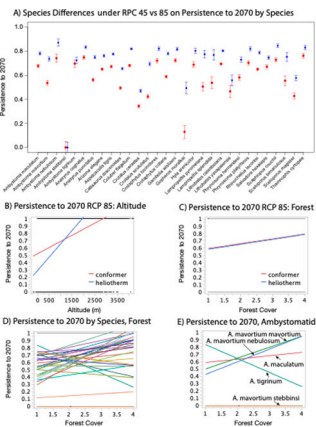
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HIGHLIGHTS

- Species distributions are shifting poleward and to higher elevations.
- Ecophysiological models identified changes in distribution of 30 desert species.
- Warmer future climates threaten at least three iconic species.
- Extinctions of species are attenuated by presence of forests and montane environments.
- The model facilitates location of new reserves and expansion of existing reserves.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Rafael Mateo Soria

Keywords:
Acclimation
Climate change
Ecophysiology
Ectotherm
Extinction model

ABSTRACT

Recent climate change should result in expansion of species to northern or high elevation range margins, and contraction at southern and low elevation margins in the northern hemisphere, because of local extirpations or range shifts or both. We combined museum occurrence records from both the continental U.S. and Mexico with a new eco-physiological model of extinction developed for lizard families of the world to predict the distributions of 30 desert-endemic reptile and amphibian species under climate change scenarios. The model predicts that 38 % of local populations will go extinct in the next 50 years, across all 30 species. However, extinctions may be attenuated in forested sites and by the presence of montane environments in contemporary ranges. Of the 30 species, three were at very high risk of extinction as a result of their thermal limits being exceeded, which illustrates the predictive value of ecophysiological modeling approaches for conservation studies. In tandem with global strategies of limiting CO₂ emissions, we propose urgent regional management strategies for existing and new reserves that are targeted at three species: Barred Tiger Salamander (Ambystomatidae: *Ambystoma mavortium stebbinsi*), Desert Short-horned Lizard (Phrynosomatidae: *Phrynosoma ornativittatum*), and Morafka's Desert Tortoise (Testudinidae: *Gopherus morafkai*), which face a high risk of extinction by 2070. These strategies focus on assisted migration and preservation within climatic refugia, such as high-elevation and forested habitats. We forecast where new reserves should be established by merging our model of extinction risk with gap analysis. We also highlight that acclimation (i.e., phenotypic plasticity) could ameliorate risk of extinction but is rarely included in ecophysiological models. We use *Ambystoma* salamanders to show how acclimation can be incorporated into such models of extinction risk.

1. Introduction

Global climate change is a pervasive threat to plants and animals in nearly all biomes and ecosystems (Garcia et al., 2014). Organisms may exhibit three responses to changing climatic regimes. First, given sufficient time and dispersal abilities, species distributions may shift to more favorable thermal environments. Second, organisms may adjust to the new local environments either by acclimation (i.e., as an example of plasticity) or adaptive evolutionary responses. The third and final response is a failure to cope with the new climatic conditions resulting in extirpation of local populations or extinction of entire species. These latter outcomes raise the issue of human-assisted approaches to rescue species (Hoegh-Guldberg et al., 2008; Paget et al., 2023). Whereas there is evidence of climate change affecting species range limits and phenology in a diversity of taxa (Vitasse et al., 2021; Cohen et al., 2018; Cohen et al., 2019; Li et al., 2013), evidence of extinctions due to anthropogenic climate change at a regional scale across continents is limited (Román-Palacios and Wiens, 2020; Urban, 2015). In addition, current forecasting models (Deutsch et al., 2008; Tewksbury et al., 2008) are not calibrated with actual extinctions (Araújo et al., 2005), rather they are based on predicted effects of thermal physiology on demographic variables, and predictions of ensuing demographic

change on local population extinction probabilities. An alternative set of models are based on range shifts, species-area relationships (Thomas et al., 2004), or mechanistic thermal physiological models (Harte et al., 2004; Lara-Reséndiz et al., 2015; Rohr et al., 2013). The variability in approaches to forecasting climate change effects have generated considerable debate over the expected magnitude of extinctions (Harte et al., 2004; Nadeau and Urban, 2019; Thomas et al., 2004; Urban, 2015). Empirical validation of biotic impacts of climate requires evidence that observed extinctions are tied to macroclimate events and explicit ground-truthed studies of microclimate effects linked to demographic processes (Sinervo et al., 2018). Furthermore, linking extinction to changing thermal regimes [e.g., biophysical thermal cause (Kearney et al., 2009)] requires demonstration that thermal physiology (Harte et al., 2004) is compromised by the pace of current climate change. Rates of evolution often lag behind the pace of climate change (Huey et al., 2003), because of constraints on the ability of phenotypic plasticity to cope with extreme thermal variation (Buckley and Kingsolver, 2021; Rohr and Palmer, 2013; Rohr et al., 2018; Sauer et al., 2018) and on the pace at which thermal adaptations can evolve (De Meester et al., 2018; Etterson and Shaw, 2001). We present a model that addresses critiques of previous models (Harte et al., 2004; Thuiller et al., 2004), because our approach verifies

that predicted extirpations are governed by mechanisms of thermal physiology and behavioral thermoregulation (Sinervo et al., 2010). A growing number of approaches for extending correlative models by integrating physiological variables have been introduced in recent years (Evans et al., 2015). These models adopt a hybrid approach (also referred to as a fusion model) by adding a physiological layer to the standard bioclim variables (e.g., Rubalcaba et al., 2019). Other approaches, such as those that include energetic traits require substantial information on physiological traits that are often unavailable for most species (see Evans et al., 2015). In our model, we include data on hours of restriction in activity, acclimation capacity of a species and mode of thermoregulation. We thus extend and generalize a model for ectothermic lizards (Sinervo et al., 2010) to other ectotherms, including snakes, amphibians, and a tortoise species, all with ranges in Mexico, Texas, Arizona, New Mexico or California. Details of our approach are given below.

Many species of reptiles use behavior to regulate their body temperatures within a narrow range. In most instances, reptiles bask by exposing their body to solar radiation to attain body temperatures that optimize physiological performance (Huey and Stevenson, 1979; Huey, 1982; Porter and Tracy, 1983; Porter, 1989). Such species will also retreat to cooler microclimates during the hottest part of the day to avoid overheating. We refer to diurnal species using behavioral thermoregulation as “heliotherms.” Other reptiles occur in habitats, e.g., dense forests with limited solar radiation, where opportunities for thermoregulation (e.g., basking) are so limited that their body temperatures follow ambient temperatures. These habitats have low thermal heterogeneity, and the cost of thermoregulation exceeds the benefits (Huey and Slatkin, 1976; Vickers et al., 2011). Snakes (Huey et al., 1989) and amphibians can thermoregulate (Lillywhite, 1970), such that their body temperatures may be somewhat higher than ambient air temperatures. However, most are nocturnal and thus are considered to “conform” their body temperature (T_b) to ambient temperature while active. In both heliotherms and conformers, activity during hot weather could result in T_b exceeding their critical thermal maxima (CT_{max}) resulting in death. In localities or seasons where ambient temperature exceeds CT_{max} , vertebrate ectotherms retreat to thermal refugia on a daily basis, or on a seasonal basis (e.g., aestivation), rather than risk death from overheating. However, longer time intervals spent in retreat sites reduces time for other activities including territorial defense, reproductive behaviors, and foraging opportunities.

We hypothesize that rising ambient temperatures due to climate change will constrain reproductive and foraging opportunities and elevate the risk of mortality through metabolic meltdown (Huey and Kingsolver, 2019). The consequence of rising temperatures exceeding limits of thermoregulatory plasticity and adaptation is the demographic collapse of a population culminating in local extinction (Paranjpe et al., 2013; Sinervo, 1990; Sinervo et al., 2010). In an analysis of the Cleft Lizard (Phrynosomatidae: *Sceloporus mucronatus*) in Mexico, during a severe warm spell in 1998, females ceased reproduction, causing extirpations in several adjacent populations (Sinervo et al., 2011). In particular, our analysis used the hours of restriction (h_r), i.e., the reduction in the number of hours of activity due to environmental temperatures exceeding the thermal limits of the species (see below). In past models (Sinervo et al., 2010), we considered the limits on adaptation. In this study, we extend our model to include thermal acclimation, which might mitigate the severity of future climate warming (Raffel et al., 2013; Rohr and Raffel, 2010; Rohr et al., 2018).

Several recent studies have examined how physiological acclimation may modify an ectothermic species' ability to persist during episodes of elevated temperatures (Markle and Kozak, 2018; Riddell et al., 2018; Rohr et al., 2018; Morley et al., 2019; Carilo Filho et al., 2022). The conclusions about the ability of acclimation to rescue species from hotter environments emerging from these studies are mixed. One study comparing the acclimation capacity in the upper thermal limit (CT_{max}) to warmer environments in amphibians and reptiles found no evidence

that such species would gain prolonged persistence in hotter conditions (Morley et al., 2019). In contrast, a meta-analysis showed a positive effect of acclimation temperature on CT_{max} on frogs, salamanders, and lizards (Carilo Filho et al., 2022). Furthermore, a mechanistic niche model that included physiological acclimation resulted in a reduced risk of extinction in salamanders (Riddell et al., 2018). Whereas these earlier studies focused on the ability of acclimation to induce an increase in CT_{max} (but see Riddell et al., 2018 for an alternative approach), our model uses changes in the number of hours of activity (h_a) and hours of restriction (h_r) as a consequence of acclimation capacity. Thus, we predict that shifts in h_a or h_r may buffer species from extinction due to climate change.

Future climate scenarios sometimes indicate the projected temperatures within the current range of a species may lead to the extirpation of local populations or even global extinction. In such instances assisted migration or translocation strategies may be necessary to protect the species. Assisted migration, sometimes known as assisted colonization, is defined as “the deliberate translocation of species from unsuitable to suitable regions” (Mitchell et al., 2013). This controversial technique can theoretically be used to prevent the extinction of species or populations that are unable to migrate from unfavorable to more favorable habitats in response to changing climatic conditions (Peterson and Bode, 2020). Although the concept is not new, having been proposed in 1985, the first known vertebrate moved from its historical range because of climate change occurred in 2022 (Watson, 2023). Forty-one juvenile western swamp tortoises (*Pseudemys umbrina*) were raised in a captive breeding program and released into a national park in Australia 330 km south of where they naturally occur. With fewer than 70 adults surviving in two small, threatened wetland reserves, they are Australia's rarest reptile. Rising temperatures and reduced rainfall are drying ponds in their native range, and researchers hope that assisted migration will be a hedge against extinction (Watson, 2023).

The goals of our study were to: (1) Estimate the hours of restriction based on contemporary climate data; (2) use future climate projections to identify populations/species at risk of local and global extirpation; (3) assess the potential for assisted migration to prevent the global extinction of those species identified by our model as at risk of extinction. The ultimate aim of the extinction analyses of the focal taxa (such as those in the Desert Landscape Conservation Cooperative or DLCC) is to provide data for developing a plan for species threatened by climate change using gap analysis (Scott et al., 1993). Gap analysis identifies missing regions of protection for diverse species under threat of extirpation and here we incorporate ecophysiological limits in reserve design. Gap analysis (Scott et al., 1993) typically includes analyses of contemporary ranges, but we use our model to highlight how assisted migration might be used to target particular sites that are protected under RCP scenarios. In tortoises, assisted migration sites in the eastern and northern extralimital margin would greatly enhance probability of persistence under the 2070 RCP scenario.

2. Methods

2.1. Taxa included in the model

We assembled an extensive database of occurrence records ($N = 30,163$) obtained from museum records (vertnet.org, CONABIO, UNAM) and USFWS reports of endemic and widespread desert-adapted amphibian and reptile species ($N = 30$) (Fig. 1). We obtained records of body temperature (T_b) and thermal preference (T_{pref}) on 30 species in the lizard families Crotaphytidae, Phrynosomatidae, and Teiidae, which were published in Sinervo et al. (2010). In addition, we present thermal data from field research in Mexico and the U.S. conducted during 2010 to 2017 (Table 1) on the snake families Colubridae and Viperidae, various amphibian families, Ambystomatidae, Bufonidae, Pelobatidae, and Ranidae, as well as one species of tortoise in the family Testudinidae. The species we included in this study are drawn from taxa that span

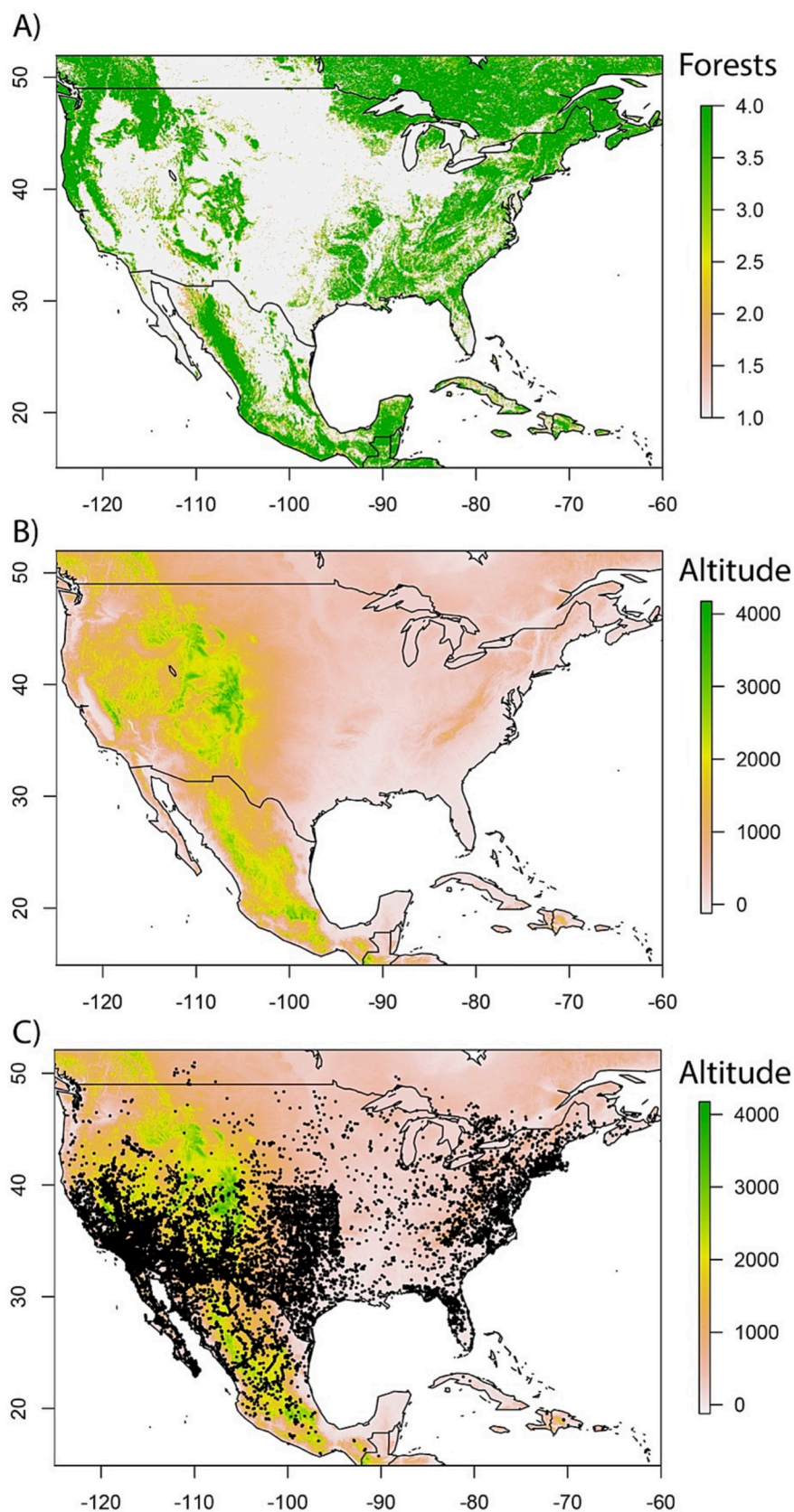


Fig. 1. The two geographic covariates used in our analysis of extinction risk: A) level of forest cover, coded 1–4, B) altitude (m) and C) density plot of occurrence records (black dots).

Table 1

Taxa and rationale for study by the Desert Landscape Conservation Cooperative.

Scientific name	Class	Family	Common name	Rationale for vulnerability assessment
<i>Ambystoma maculatum</i>	Amphibia	Ambystomatidae	Spotted Salamander	Treated as a species complex for modeling
<i>Ambystoma mavortium</i>	Amphibia	Ambystomatidae	Western Tiger Salamander	Treated as a species complex for modeling
<i>Ambystoma nebulosum</i>	Amphibia	Ambystomatidae	Western Tiger Salamander	Treated as a species complex for modeling
<i>Ambystoma stebbinsi</i>	Amphibia	Ambystomatidae	Sonoran Tiger salamander	Treated as a species complex for modeling, listed as Endangered, USFWS
<i>Ambystoma tigrinum</i>	Amphibia	Ambystomatidae	Eastern Tiger Salamander	Treated as a species complex for modeling
<i>Anaxyrus cognatus</i>	Amphibia	Bufonidae	Great Plains Toad	Widespread; reliant on temporary ponds; sensitive to drought
<i>Anaxyrus punctatus</i>	Amphibia	Bufonidae	Red-spotted Toad	Widespread; talus habitat; reliant on temporary and permanent water sources
<i>Arizona elegans</i>	Reptilia	Colubridae	Glossy Snake	Widespread; lowland
<i>Aspidoscelis tigris</i>	Reptilia	Teiidae	Tiger Whiptail	Widespread
<i>Callisaurus draconoides</i>	Reptilia	Phrynosomatidae	Zebra-tailed Lizard	Fairly widespread
<i>Coluber flagellum</i>	Reptilia	Colubridae	Coachwhip	Fairly widespread
<i>Crotalus cerastes</i>	Reptilia	Viperidae	Sidewinder	Habitat specialist restricted to sandy areas
<i>Crotalus scutulatus</i>	Reptilia	Viperidae	Mohave Rattlesnake	Recent range expansion eastward
<i>Crotaphytus bicinctores</i>	Reptilia	Crotaphytidae	Great Basin Collared Lizard	Mojave, Sonoran Deserts
<i>Crotaphytus collaris</i>	Reptilia	Crotaphytidae	Eastern Collared Lizard	Fairly widespread
<i>Gambelia wislizenii</i>	Reptilia	Crotaphytidae	Long-nosed Leopard Lizard	Widespread
<i>Gopherus morafkai</i>	Reptilia	Testudidae	Sonoran Desert Tortoise	Iconic species; candidate for FWS listing
<i>Hyla arenicolor</i>	Amphibia	Hylidae	Canyon Treefrog	Chihuahuan/Sonoran long north-south range
<i>Lampropeltis pyromelana</i>	Reptilia	Colubridae	Arizona Mountain Kingsnake	Treated as a species complex for comparing montane versus lowland species
<i>Lampropeltis splendida</i>	Reptilia	Colubridae	Desert Kingsnake	Treated as a species complex for comparing montane versus lowland species
<i>Lithobates catesbeianus</i>	Amphibia	Ranidae	American Bullfrog	Non-native species; invasive and disruptive to amphibian
<i>Lithobates yavapaiensis</i>	Amphibia	Ranidae	Lowland Leopard Frog	Widespread, extirpated from California and Nevada
<i>Phrynosoma hernandesi</i>	Reptilia	Phrynosomatidae	Greater Short-horned Lizard	Treated as a species complex for modeling with <i>P. douglasii</i> (Montanucci, 2015) montane, wide-ranging north (Canada) to south (México)
<i>Phrynosoma platyrhinos</i>	Reptilia	Phrynosomatidae	Desert Horned Lizard	Widespread; lowland
<i>Rhinocheilus lecontei</i>	Reptilia	Colubridae	Long-nosed Snake	Widespread
<i>Salvadora hexalepis</i>	Reptilia	Colubridae	Western Patch-nosed Snake	Widespread, many habitats
<i>Scaphiopus couchii</i>	Amphibia	Pelobatidae	Couch's Spadefoot	Widespread; sporadic appearance
<i>Sceloporus bimaculosus</i>	Reptilia	Phrynosomatidae	Twin-spotted Spiny Lizard	Treated as a species complex for comparing response in geographically proximate and genetically related species, <i>Sceloporus magister</i>
<i>Sceloporus magister</i>	Reptilia	Phrynosomatidae	Desert Spiny Lizard	Treated as a species complex for comparing response in geographically related taxa
<i>Thamnophis cyrtopsis</i>	Reptilia	Colubridae	Black-necked Gartersnake	AZ, NM, W TX, ranging south to Guatemala, many habitat types

the Desert Landscape Conservation Cooperative region (lccnetwork.org) list of sensitive species. Our rationale for species selection is given in Table 1. We also assembled data on elevation and amount of forest cover for all geo-referenced locations and analyze these geographic factors that might ameliorate extinction risk based on their interaction with thermal physiology.

2.2. A global model of extinction risk for lizards applied to reptile and amphibian biodiversity

The utility of an extinction model of eco-physiology is reflected in the set of parameters used to predict extinction risk. First, a climate change surface is required. Contemporary (1975, worldclim.org) and future climate surfaces (2050, 2070, RCP 45 and 85) can be used to predict maximum air temperature (T_{max}) at any geographic site at time points in the future, and thus can be used to predict impacts on extinction risk. In those species that use behavioral thermoregulation to adjust their body temperature (hereafter heliotherms; e.g., Sauer et al., 2019) a restriction in their activity while basking exceeding the species-specific critical hours of restriction (hours per day, h/d), would result in classifying a

focal population as locally extinct (Ceia-Hasse et al., 2014; Kubisch et al., 2015; Lara-Reséndiz et al., 2015; Rohr and Palmer, 2013). Time of activity has been shown to be a better predictor of a species presence in a site than environmental temperatures alone (Caetano et al., 2020). The development of our eco-physiological model requires data on mean active body temperatures, environmental temperatures, and future climate scenarios to generate estimates of extinction risk for reptiles and amphibians.

2.3. Reptile and amphibian body temperatures, and patterns of behavioral thermoregulation

We obtained values for body temperature from the literature and our own studies (Table 2). The T_b data are not only from heliotherms, such as lizards in the family Phrynosomatidae, but are also from conformers that do not bask and whose body temperatures often track ambient temperature (Huey, 1982). We averaged all published field T_b records with T_{pref} values to obtain a single species-specific measure for T_b and T_{pref} , hereafter referred to as T_b [T_b and T_{pref} have a high correlation (see SOM Sinervo et al., 2010)]. We coded species as either heliotherms or

Table 2

Taxa in Desert Landscape Conservation Cooperative (DLCC): mean field active body temperature (T_b), thermoregulatory mode used extinction-risk models, source, and computed $h_{r,critical}$ (95 % quantile for h_r values computed for the contemporary period at site occurrence records).

Species	Thermoregulatory mode	T_b	$h_{r,critical}$	Source
<i>Ambystoma maculatum</i>	Conformer	11.1	24.0	(Keen and Schroeder, 1975)
<i>Ambystoma mavortium</i>	Conformer	18.6	13.2	naherp.com records for AZ, NM, TX
<i>Ambystoma mavortium nebulosum</i>	Conformer	18.5	8.5	naherp.com records for AZ, NM, TX
<i>Ambystoma mavortium stebbinsi</i>	Conformer	18.5	10.6	naherp.com records for AZ, NM, TX, average of parental species
<i>Ambystoma tigrinum</i>	Conformer	15.5	21.0	naherp.com, range wide
<i>Anaxyrus cognatus</i>	Conformer	23.1	12.7	(Sullivan, 1983)
<i>Anaxyrus punctatus</i>	Conformer	28.4	7.8	DLCC research
<i>Arizona elegans</i>	Conformer	21.2	14.5	(Brattstrom, 1965)
<i>Aspidoscelis tigris</i>	Heliotherm	39.3	1.9	Sinervo et al., 2010 SOM
<i>Callisaurus draconoides</i>	Heliotherm	38.7	2.3	Sinervo et al., 2010 SOM
<i>Coluber flagellum</i>	Conformer	31.6	2.7	(Brattstrom, 1965)
<i>Crotalus cerastes</i>	Conformer	25.8	10.4	(Brattstrom, 1965)
<i>Crotalus scutulatus</i>	Conformer	30.0	4.9	(Brattstrom, 1965)
<i>Crotaphytus bicinctores</i>	Heliotherm	36.3	3.9	Sinervo et al., 2010 SOM
<i>Crotaphytus collaris</i>	Heliotherm	36.3	3.6	Sinervo et al., 2010 SOM
<i>Gambelia wislizeni</i>	Heliotherm	38.2	3.4	Sinervo et al., 2010 SOM
<i>Gopherus morafkai</i>	Heliotherm	35.0	1.0	DLCC Research, Sonora Mexico
<i>Hyla arenicolor</i>	Conformer	30.7	4.6	(Warburg, 2012)
<i>Lampropeltis pyromelana</i>	Conformer	25.1	6.0	Bryan Hamilton pers. comm.
<i>Lampropeltis splendida</i>	Conformer	28.1	8.0	(Brattstrom, 1965)
<i>Lithobates catesbeianus</i>	Conformer	28.1	2.7	(Lillywhite, 1970)
<i>Lithobates yavapaiensis</i>	Conformer	26.2	10.1	(Platz and Frost, 1984)
<i>Phrynosoma hernandesi</i>	Heliotherm	33.0	2.4	Sinervo et al., 2010 SOM
<i>Phrynosoma platyrhinos</i>	Heliotherm	36.0	3.1	Sinervo et al., 2010 SOM
<i>Rhinocheilus lecontei</i>	Heliotherm	25.2	11.8	DLCC research
<i>Salvadora hexalepis</i>	Conformer	29.6	6.4	DLCC research
<i>Scaphiopus couchii</i>	Conformer	19.8	20.1	generic average (Fouquette Jr, 1980)
<i>Sceloporus bimaculosus</i>	Heliotherm	34.9	4.6	Sinervo et al., 2010 SOM
<i>Sceloporus magister</i>	Heliotherm	34.9	4.6	Sinervo et al., 2010 SOM
<i>Thamnophis cyrtopsis</i>	Conformer	26.4	11.3	(Brattstrom, 1965)

conformers based on published patterns of their thermal physiology, or our own observations during data collection (Table 2). For conformers, we also used the published model for conforming families (Sinervo et al., 2010). Conformers are close to T_{air} during the day or night.

2.4. Operative environmental temperatures

We used operative temperature (biomimetic) models (Bakken and

Gates, 1975) to estimate operative environmental temperatures (T_e) deployed at sites within the region included in the Desert Landscape Conservation Cooperative: Mojave, Sonoran, and Chihuahuan, Deserts. Although many of the species included in our study have ranges extending beyond the DLCC, such as the Short-horned Lizard (*Phrynosoma hernandesi*, Phrynosomatidae) complex that is found from Mexico to Canada, we restricted our model to T_e data from the arid regions of the southwestern United States and northern Mexico. Here we use sets of four models developed for reptiles of various sizes, and tortoises spanning montane forests and deserts sites ($N = 80$ sites). We deployed sensors at sites spanning northern Arizona, central New Mexico, southeastern California and south to central Mexico. At each site, we randomly placed a minimum of four sensors, with two in open and two in shaded microhabitats known to be used by the focal species (for more details, see Lara-Resendiz et al., 2014; Lara-Resendiz et al., 2015). Each PVC model was validated against body temperatures for small ectotherms (Lara-Resendiz et al., 2014; Lara-Resendiz et al., 2015; Sinervo et al., 2010).

We also developed a novel continuous-time monitoring system at three University of California Natural Reserve Sites (Granite Mountains NRS, Boyd Deep Canyon NRS, and Elliot Chaparral NRS) and six sites in the Southwest Experimental Garden Array of Northern Arizona University (SEGA, www.sega.nau.edu). At each of sites, we monitored a total of 36 operative temperature models constructed of polyvinyl-chloride (PVC) tubes of three different sizes, in diverse habitat types where reptiles occur (see below). Thus, each site had 12 models in each of the three size classes. The full analysis of T_e data will be presented elsewhere.

Depending on presence of heliothermic taxa of different sizes in a local habitat, we deployed small (10×1.25 cm) and medium PVC models (15×2.5 cm) suitable for computing constraints of hours of restriction on small and medium-sized lizards in the family Phrynosomatidae (Sinervo et al., 2011), as well as medium-large (22×4 cm) and large PVC models (25×6 cm), all painted grey, suitable for computing hours of restriction in large-bodied heliothermic lizards in the family Crotaphytidae. For horned lizards (Phrynosomatidae: *Phrynosoma* spp.), we used flattened PVC models (Lara-Resendiz et al., 2014; Lara-Resendiz et al., 2015). For tortoises, we constructed sealed copper models of the same size and shape of tortoise species in the genus *Gopherus* and deployed them at sites where they occur across the US and Mexico spanning Desert habitats (See Lara-Resendiz et al., 2022a, 2022b). We used two-channel Hobo® Pro v2 data loggers (Onset Computer, Bourne, Massachusetts) to record T_e data. Sensors were placed within each PVC operative temperature model and affixed to avoid touching the inner walls of the model. Data loggers recorded temperature every 30 min.

The values of T_e are used in the model to calculate the number of hours of restriction or hours of activity. While the models continuously collected temperature data, we used only the data during the general breeding season for this study, which was defined from March 1st to July 31st.

2.5. Acclimation capacity

In our previous model of extinction risk (Sinervo et al., 2010), we assumed that thermal physiology of ectothermic vertebrate species would be static, given that heritability for thermal preference is too low to exhibit a swift evolutionary response under current climate warming trends (Logan et al., 2018; Paranjpe et al., 2013; Sinervo, 1990; Sinervo et al., 2010). However, some species of amphibians can adjust either their thermal preference (T_{pref}) or critical thermal maximum (CT_{max}) to higher values after acclimation to a warmer temperature (Li et al., 2013; Rohr et al., 2018). Acclimation experiments on reptiles have shown lower capacities to adjust thermal traits (e.g., Morley et al., 2019). Here, we include acclimation capacity in our model, which complements the previous version of our model that only considered an evolutionary

response to selection (e.g., adaptation to warming) (Sinervo et al., 2010). We assume that the number of hours of restriction per day that results in population decline, $h_{r, \text{critical}}$, would remain the same as that observed during the contemporary period. However, a species might exploit a plastic response to warmer temperatures by adjusting its T_b upwards to acclimate to warmer environments. This has the effect that the h_r computed for a given site, across a given period, such as the breeding (and larval) period used herein, would be lowered, thus rescuing the population from extirpation.

To parameterize the magnitude of possible response to climate warming, we assume an acclimation capacity of 2.5–4 °C for the increase in T_{pref} or CT_{max} , which was largely conducted at acclimation temperatures between 5 and 20 °C (see Brattstrom and Lawrence, 1962; Rohrer et al., 2018). We show below that a complete rescue from climate change will require acclimation capacities on the order of 5–6.5 °C, but few studies have been conducted at acclimation temperatures >25 °C, which may be required for a species to be buffered against climate warming.

2.6. Estimating h_r and h_a

We computed the hours of restriction for each species in the Desert Landscape Conservation Cooperative (DLCC) using a sigmoidal eq. (4-parameter Richards Growth Curve; see Lara-Reséndiz et al., 2022a) that relates h_r to the climate variable T_{max} and the physiological trait, T_b ($T_{\text{max}} - T_b$). Examples of these curves for hours of restriction and hours of activity are presented in Fig. 2A for Agassiz's Desert Tortoise (Testudinidae: *Gopherus agassizii*). If the computed value of h_r exceeded the species' $h_{r, \text{critical}}$ (the number of hours of restriction per day that results in population decline), we assumed the focal population would be extirpated.

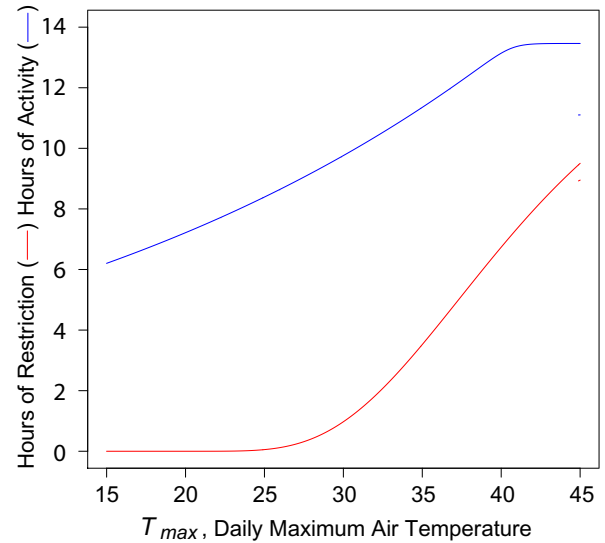
In computing the $h_{r, \text{critical}}$ we followed the method outlined in Caetano et al. (2020). We modeled daily air temperature variation as a sinusoidal curve between the maximum and minimum daily air temperatures per each location using the relevant rasters extracted from Worldclim. To analyze the pattern for conformers, we first computed daily excursions in T_{min} to T_{max} climate rasters (average of April–June T_{min} and T_{max}), as a sine wave for T_{air} with a 24 h amplitude and integrated (numerically) the hours of restriction in activity as the times when $T_e > T_b$. An example h_r curve for a heliotherm is shown for Morafka's Desert Tortoise (*Gopherus morafkai*) in Fig. 2B. To estimate a measure of the critical hours of restriction, $h_{r, \text{critical}}$, for each species we used the 95 % quantile of h_r values, similar to the model developed for lizard families (Sinervo et al., 2010).

For both heliotherms and conformers, one can also compute the number of hours of activity as the period during the normal activity period (e.g., nocturnal, diurnal or cathemeral), when $T_e > \text{minimum voluntary and maximum voluntary } T_b \text{ for activity} < T_e$ observed for each species. One may use either T_e from the operative temperature models for heliotherms or the sine wave for T_{air} for thermal conformers. We refer to this quantity as hours of activity or h_a . This value provides an estimate of the time available for activity for each species at each locality.

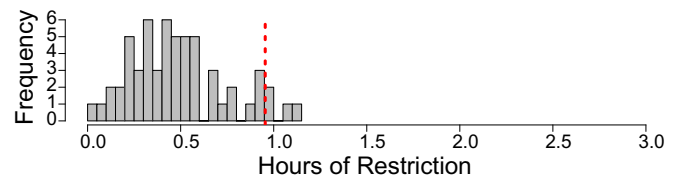
2.7. Current and future climate data

We used contemporary climate layers (1950–2000, average 1975) and future climate layers from worldclim.org (Fick and Hijmans, 2017) to compute the critical hours of restriction, h_r . For climate layers, we used the MPI-ESM-LR (Max Planck Institute Earth System Model) at 1.8758 degrees resolution (downscaled to 1 × 1 km grid cells) under 2 models of Representative Concentration Pathways (RCPs) assuming +4.5, and +8.5 W/m², hereafter referred to as RCP 45 and RCP 85, for the decades of 2040–2060 and 2060–2080, hereafter referred to as 2050 and 2070. We obtained values of h_r for all geo-referenced locations of a given species and used this eco-physiological metric to predict

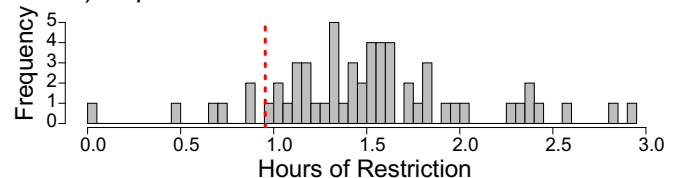
A) Functions for hours of restriction and activity



B) *Gopherus morafkai*: Contemporary 1975



C) *Gopherus morafkai*: 2070 RCP 85



D) *Gopherus morafkai*: 2070 RCP 45

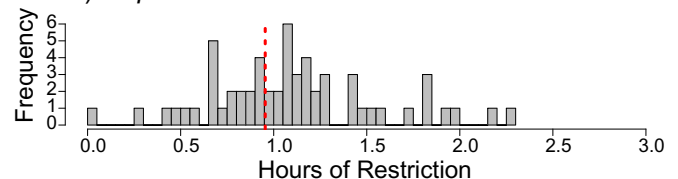


Fig. 2. Dependence of the hours of restriction (h_r , red lines) and hours of activity (h_a , blue lines) on T_{max} (daily maximum air temperature) for A) *Gopherus agassizii* in desert habitats (data analyzed from Zimmerman et al., 1994). Application of the h_r curve to $T_{\text{max}} - T_b$ for the B) contemporary (1975), under C) 2070 RCP 85 and D) 2070 RCP 45. In B–D the dashed red line represents the critical h_r (95 % quantile) used to simulate the upper eco-physiological limit for extinctions in future periods for *Gopherus morafkai*. Values of h_r above the dashed red line are assumed to go extinct.

extinction at future scenarios points (RCP 45, 85, 2050, 2070). The h_r values integrate T_b and operative environmental temperatures (T_e) data in the case of heliotherms, or T_b and ambient temperature in the case of thermoconformers. This ensemble of models captures observed patterns of temperature and precipitation during the control period (Anav et al., 2013), and thus may be better able to predict future climate change. For all climate surfaces, geographic covariates, and species occurrence records (Fig. 1C), we used a spatial extent of longitude = [−125°, −65°], latitude = [15°, 52°] to span all known occurrence records of the chosen taxa (Table 1, Fig. 1C), and a grid size of 30 arc-sec (~1 × 1 km).

2.8. Estimates of extinction risk

If h_r of a species at a given site was predicted to exceed its $h_{r,critical}$ value, we assumed the species would be extirpated, as shown for *G. morafkai* for 2070 under RCP 85 and RCP 45 scenarios (Fig. 2). If a species was predicted to be extirpated across 95 % of all known occurrence sites, we considered it to be at high risk of total species-level extinction. We previously calibrated this $h_{r,critical}$ criteria for extinction against observed extinctions in 8 families of heliothermic or thermoconforming reptiles (Sinervo et al., 2010, 2011).

2.9. Predictors of extinction (extirpation) risk

To develop geographic and climate estimates of extinction risk, we used logistic regression analysis (e.g., predicted to be extinct = 0 vs. persistent = 1), ignoring phylogeny, but including geographical covariates and factors for either species or family. Analysis of species-level occurrence records in a geographic framework is useful for land managers that can target specific populations and species (at risk of extirpation or extinction) with proactive delineation of new reserves that focus on refugia from climate extremes, such as sites at high elevation and/or with forest cover (Fig. 1A, B). We use logistic regression with extinction risk and a set of predictor variables that are expected to influence the persistence of species, e.g., thermoregulatory mode (conformer vs. heliotherm), family or species, and their interaction terms as well as two covariates, elevation and forest cover. Note: in our model, we assumed that forest cover (United Nations Environment Programme, 2016) remains intact under climate warming (and no deforestation) and that forest cover impacts h_r through its effects on T_{max} , which we analyze separately with a fitted surface involving linear and quadratic terms for forest cover and altitude, and their interaction term (forest $\times$ elevation). While logistic regression is suitable for statistical inference in the case of a binomial variable, it does not allow for easy visualization of protection that forest or elevation affords. We therefore used a general linear model to identify the potential for forest cover or elevation to alter extinction probabilities.

Eco-physiological models assume that a species is adapted to its local thermal habitats prior to climate change, and that non-random extinctions will be concentrated at warmer range boundaries, where the velocity of climate change is most rapid, or where taxa are limited either by thermal physiology or species interactions, e.g., competition, predation (Brown, 1984; Terborgh, 1973). We included mode of thermoregulation as a factor (heliotherm vs. conformer), because we hypothesized a priori that conforming animals would be at greater risk of climate-change-induced extinctions, given that previous theory and data indicate that tropical conformers are closer to their thermal limits than heliotherms, because they are adapted to life in the cooler habitats afforded by closed forest canopies (Huey et al., 2009).

In addition, recent manipulations of vegetation cover indicate an ameliorative effect on physiology and behavioral thermoregulation in the context of warming temperatures (Sears et al., 2016). Therefore, we included forest layers into our model: ocean/water = N.A., 1 = other land cover, 2 = other wooded land, 3 = open or fragmented forest, and 4 = closed forest (Programme, 2016) (Fig. 1A).

3. Results

3.1. T_b and $h_{r,critical}$ among heliotherms and conformers

Among the reptile and amphibian species in our study, heliotherms have higher T_b than do conformers. Values of T_b and the computed value for $h_{r,critical}$ for all taxa are given in Table 2. Both T_b and $h_{r,critical}$ are significantly different for thermoconforming and heliothermic species (mean T_b = 24.3 °C versus 35.3 °C for conformers and heliotherms respectively, $F_{1,28}$ = 16.9, P < 0.00001, mean $h_{r,critical}$ = 10.0 h versus 3.9 h for conformers and heliotherms respectively, $F_{1,28}$ = 8.50, P <

0.0014). As found in our analysis of lizards of the world (Sinervo et al., 2010), conformers had a much higher $h_{r,critical}$, because they tend to be nocturnal and thus can sustain long periods of h_r in cool retreat sites when $T_{air} > T_b$ during the day, but require cool periods at night when $T_{air} < T_b$. For example, *Ambystoma maculatum* has a T_b so high relative to ambient temperatures that there are no sites where it experiences hours of restriction ($h_{r,critical}$ = 24.0) during the breeding season. While *A. maculatum* is not in the DLCC because it occurs in eastern forests, we included it as a reference point for taxa in the *A. tigrinum-mavortium* complex in the DLCC (Table 1).

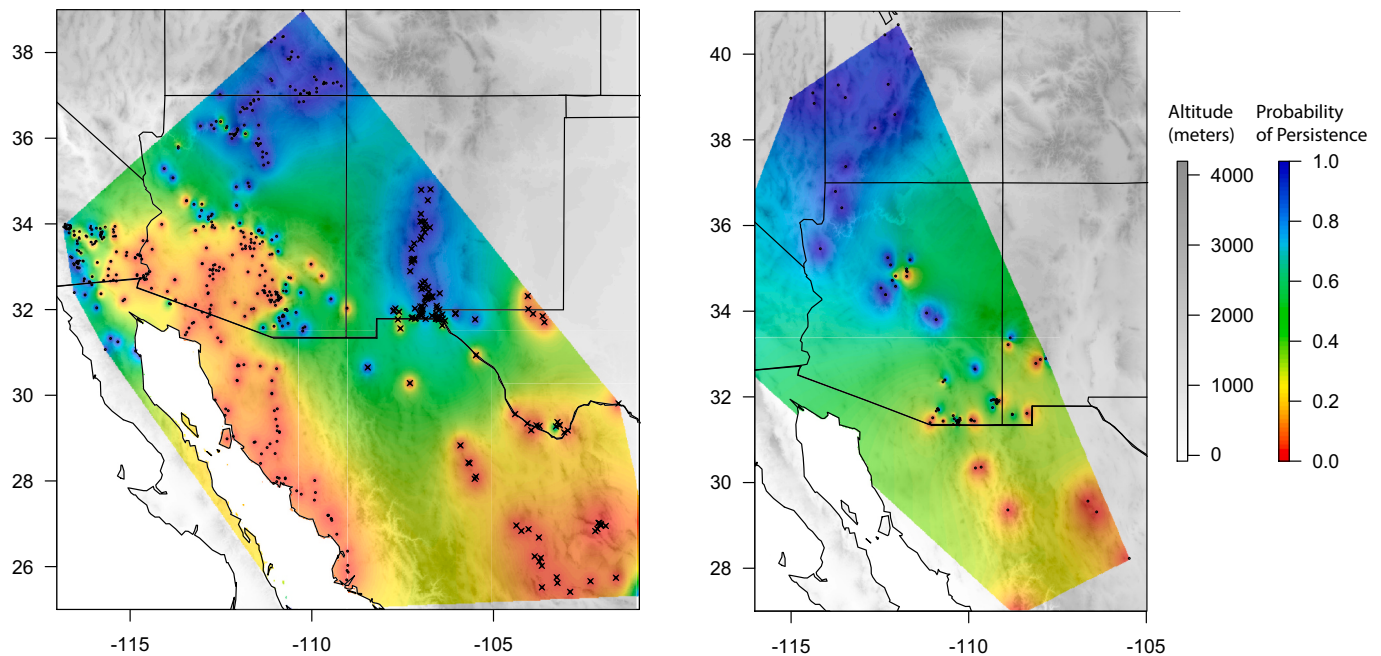
3.2. Extinction risk across the Desert Landscape Conservation Cooperative focal taxa

Geographic patterns of extinction risk for representative reptilian and amphibian species are presented in Figs. 3–6. Our analysis projects that only a single species, *Ambystoma mavortium stebbinsi*, will be totally extinct by 2070 under RCP 85 (Fig. 3). However, another species, *Gopherus morafkai*, is at grave risk of extinction by 2070 under RCP 85 (only 13 % of populations are predicted to remain) (Fig. 4) but is at a much lower extinction risk (48 %) under the RCP 45 scenario (Fig. 4). Likewise, two species in the *Phrynosoma hernandesi* species complex, as revised by Montanucci (2015), are predicted to have a high risk of extirpation. One species, *Phrynosoma ornatissimum brachycercum*, which occurs in México has a high risk of extirpation ($P_{persistence} = 0$); a second species, *Phrynosoma o. ornatissimum*, that occurs in the arid, short-grass prairies of New Mexico, is at a grave risk of extinction (Fig. 6). Although the other 27 species do not face imminent threats from climate change, we estimate 38 % of all local populations will go extinct by 2070 under RCP scenarios. We show maps for two species of related lizards, Desert Spiny Lizard (*Sceloporus magister*) and Twin-spotted Spiny Lizard (*S. bimaculosus*), and the montane Sonoran Mountain Snake (*Lampropeltis pyromelana*), to illustrate representative patterns observed across all 30 species (Fig. 3). All 27 other DLCC species have climate refugia at high elevation sites and at high latitudes, but those species with ranges extending into México are at severe risk of extinction south of the U.S. border, regardless of climate change scenario. We also highlight risks for *G. morafkai*, a tortoise (Fig. 4) that has been petitioned twice to be listed on the Endangered Species Act, *A. m. stebbinsi* (Figs. 3, 5), a species listed as Endangered by the US Fish and Wildlife Service (Hossack et al., 2016), and for *P. ornatissimum*, which faces a serious risk of extinction, particularly in México, but is not yet listed (Fig. 6).

The difference between RCP 45 and 85 for 2070 can be compared with repeated measures (RCP scenario across sites) ANOVA (Fig. 6A) to isolate species at greatest risk of extinction (2070), and which might benefit from global mitigation strategies involving atmospheric CO₂. We find that both families ($F_{10,30,152}$ = 16.049, P < 0.001) and species ($F_{29,30,133}$ = 19.135, P < 0.0001, Fig. 7A) differ significantly between RCP 45 and 85 scenarios. With the exception *Ambystoma mavortium stebbinsi*, which has a low probability of persistence regardless of RCP scenario and two other amphibian species (*Ambystoma tigrinum* and *Lithobates yavapaiensis*) the remaining 27 species all have a higher persistence to 2070 in the RCP 45 compared to RCP 85. This result indicates that some families and species benefit more from reducing greenhouse gas emissions than others.

Of the three species at greatest risk of extinction, *G. morafkai* will benefit the most under lower RCP scenarios ($P_{persistence}$ = 0.129 vs $P_{persistence}$ = 0.493 under RCP 85 vs. RCP 45, Fig. 4). *Ambystoma mavortium stebbinsi* will not benefit ($P_{persistence}$ = 0.00 vs $P_{persistence}$ = 0.00 under RCP 85 vs. 45, Figs. 3, 5), and is predicted to go extinct under both RCP scenarios. In contrast, its congeners (*A. maculatum*, *A. mavortium mavortium*, *A. mavortium nebulosum*, *A. tigrinum*) face low risk of extinction (all $P_{persistence}$ > 0.5, Fig. 6) and benefit from the RCP 45 scenario. *Phrynosoma o. brachycercum* is at risk of total extinction in México (Fig. 6A) with limited refugia in its montane habitat (Fig. 6B). In New Mexico, *P. o. ornatissimum* (Fig. 6B) is at grave risk of extinction;

A) Persistence of *Sceloporus magister* and *S. bimaculosus* to 2070 B) Persistence of *Lampropeltis pyromelana* to 2070



C) Persistence of *Ambystoma complex* to 2070, RCP 85 D) Persistence of *Ambystoma complex* to 2070, RCP 45

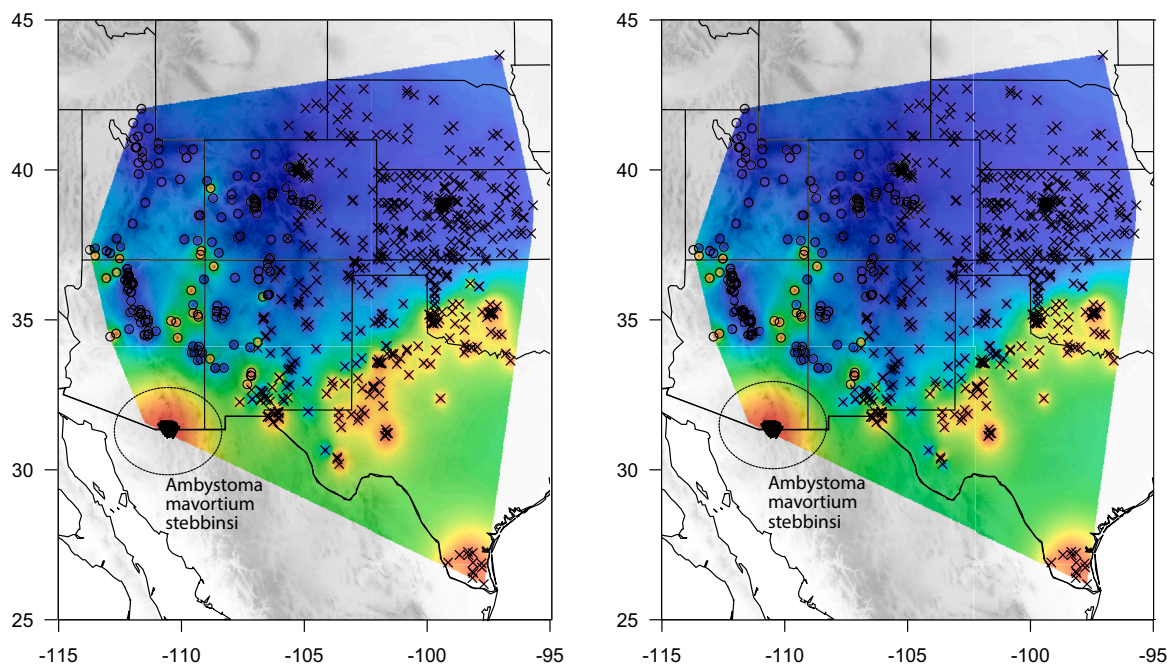


Fig. 3. Geographic patterns of persistence vs. extinction risk projected of A) the lizards, *Sceloporus magister* (•) and *S. bimaculosus* (×), B) a montane snake, *Lampropeltis pyromelana*, for 2070 RCP 85 scenario, and C–D) salamander species complex comprised of *Ambystoma mavortium mavortium* (×), *A. m. nebulosum* (○), and *A. m. stebbinsi* (inverted triangles), for both RCP 85 and RCP 45 scenarios. Examples illustrate geographic extinction patterns observed across all 30 of the study species, where we project high rates of extinction across México, but climate refugia (colored in blue) at high latitude in the U.S., and at high-elevation and forested sites. Note that the model predicts global extinction of *A. m. stebbinsi* (oval) under both scenarios.

there are montane refugia adjacent to its current distribution in western and southeastern NM, but they are occupied by *P. hernandesi*, which faces a low risk of extinction (Fig. 6B).

The overall reduction of extinction risk by decreasing greenhouse gas emission across all 30 species was on average $P_{\text{persistence}} = 0.133$ going from RCP 85 to RCP 45 (e.g., $P_{\text{persistence}} = 0.627$ vs $P_{\text{persistence}} = 0.758$).

Thus, meeting the emissions goals for RCP 45 facilitates persistence of families that are predicted by our model to be close to extinction by 2070, which represents a substantial degree of protection from climate-forced extinction (c.f., distance between means for RCP 45 vs. RCP 85, Fig. 6).

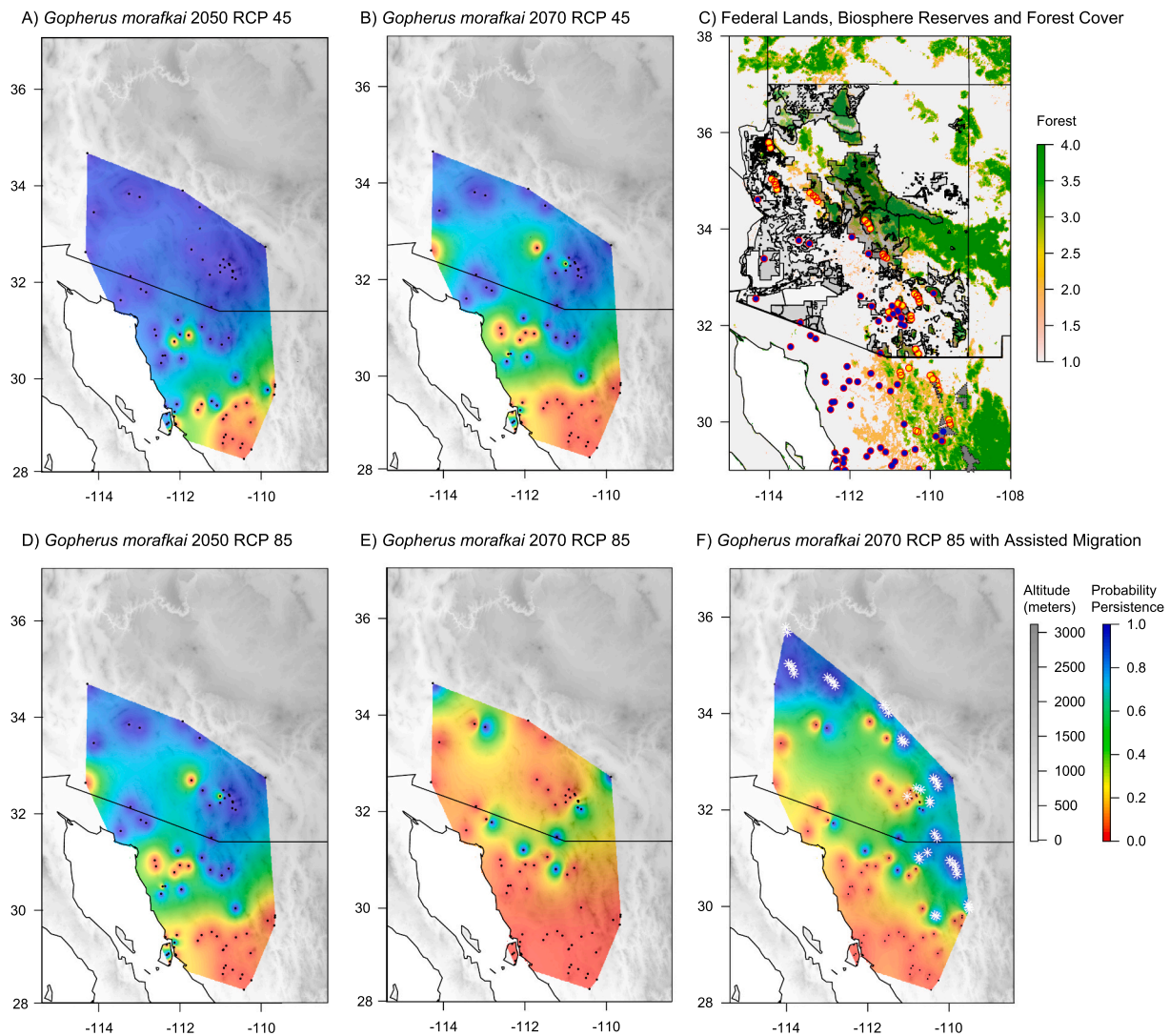


Fig. 4. Extinction risk for *Gopherus morafkai* for four climate scenarios: A) 2050 RCP 45, B) 2050 RCP 85, D) 2070 RCP 45 and F) 2070 RCP 85. Probability of persistence of contemporary local populations (●) are coded blue (1.0) and extinction are coded red (0.0). Predicted climate refugia are islands of blue (persistence = 1.0) at high elevation and forested sites. E) Predicted refuges could be sited (yellow dots) in adjacent Federal Lands in AZ and Biosphere reserves in Mexico (grey shading) and tortoises could be transplanted to them from contemporary sites (blue dots). F) We simulated assisted migration by siting tortoises (white dots) on forested and high altitude (1100–1400 m) sites located on U.S. Federal Lands and Biosphere Preserves in Mexico. Assisted migration sites are at the eastern and northern extralimital margins (white stars in panel E, yellow dots in panel C) where tortoise persistence in 2070 (panel F) is projected to be enhanced.

3.3. Extinction risk, forests, elevation, and thermoregulatory mode

Patterns of extinction risk (2070 RCP 85) across ectotherm families (and species) were differentially affected by altitude, forest cover, and thermoregulatory mode (logistic regression with altitude and forest cover as covariates, mode of thermoregulation, heliotherm vs conformer, as a factor). The biogeographic patterns of climate warming will interact with these differences in thermal physiology among taxa according to how T_{max} changes as a function of elevation and forest cover. On average moving from no forests [=1 on the standardized forest scale (United Nations Programme, 2016)] to closed forest habitats (=4) attenuates T_{max} by 2.49 °C in 1975, and by 2.88 °C in 2070, thus lowering T_e , and h_r and ameliorating extinction risk. High elevation sites that are well above 1800 m will be protected by a lower T_{max} and by a lower rate of change in T_{max} (from 1975 to 2070), thus providing robust climate refuges.

In Fig. 7, we show the patterns of extinction risk in a general linear model to allow visualization of the elevational thresholds or forest cover thresholds (the point where the regression line intersects probability of

persistence = 1), that provide a climate refuge for conformers versus heliotherms (Fig. 7B, C).

Conformers experienced lower extinction risk at low elevation sites compared to heliotherms (Fig. 7B), as supported by a significant interaction between elevation and thermoregulatory mode (logistic regression, $\chi^2 = 353.6$, $P < 0.001$). Compared to heliotherms, conformers experienced lower extinction risk at low altitude sites, but higher extinction risk at high altitude sites (Fig. 7B). Despite this interaction, the presence of forests ameliorated extinction risk in both conformers and heliotherms (Fig. 7C, logistic regression: forest cover: $\chi^2 = 316.3$, $P < 0.00001$, forest $\times$ thermoregulatory mode: $\chi^2 = 2.1$, $P > 0.14$). However, the amount of amelioration associated with forest cover depended upon species (forest cover $\times$ species: $\chi^2 = 457.2$, $P < 0.00001$, Fig. 7D).

We used the family Ambystomatidae to illustrate the variability in extinction risk in response to forest cover (Fig. 7E): forest cover increased the probability of persistence for both *A. mavortium mavortium* and *A. mavortium nebulosum*. Further, a change in forest cover had no significant impact on the persistence of *A. maculatum*, but it had a

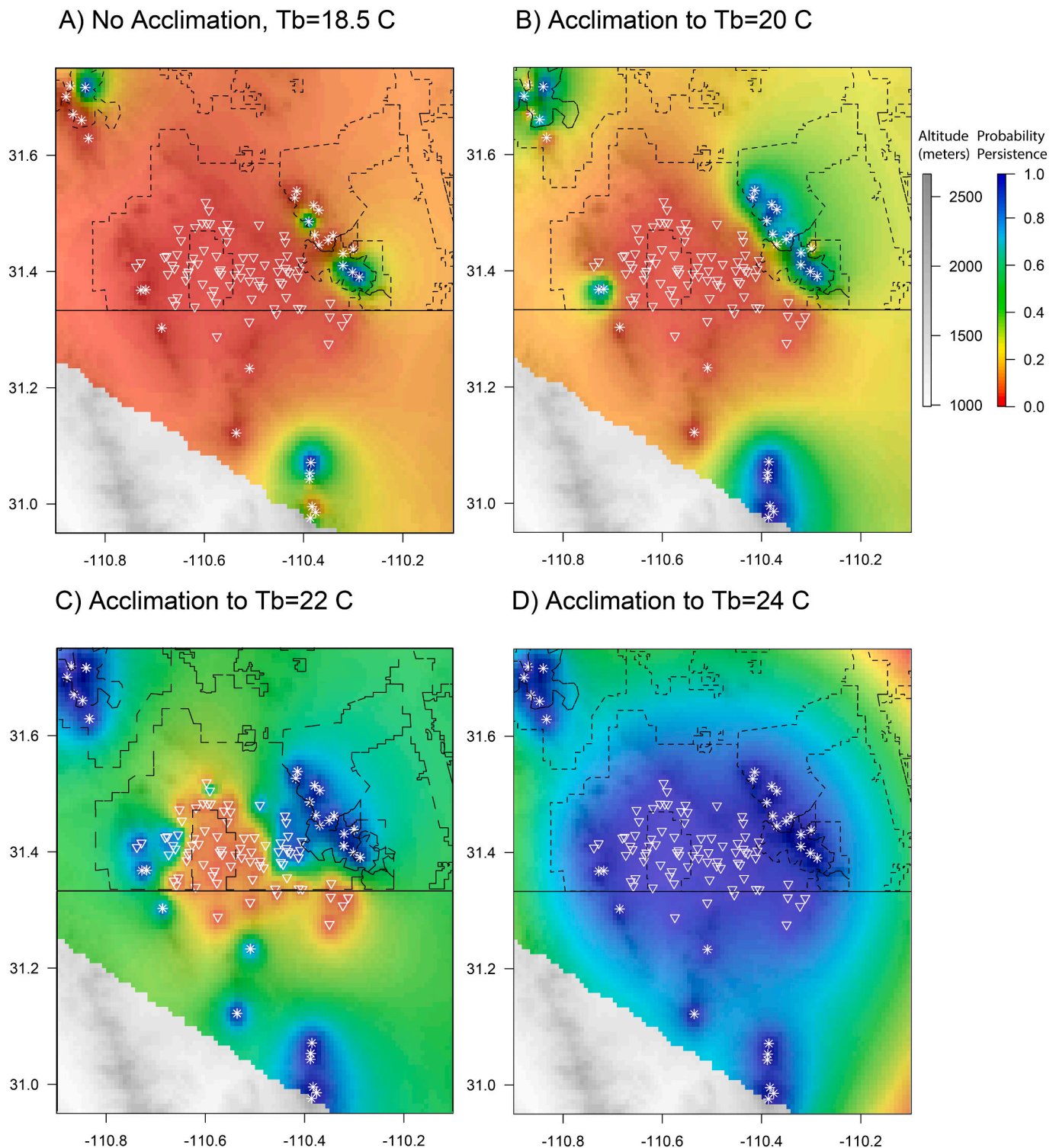


Fig. 5. Extinction risk for contemporary occurrence records of *Ambystoma mavortium stebbinsi* (inverted white triangles) in Arizona and Mexico for 2070 under RCP 85, with a sensitivity analysis for the ability of the salamander to acclimate to higher temperatures than the average body temperature ($T_b = 18.5$ °C) observed in the contemporary period, and at assisted migration sites (denoted by white stars): A) no acclimation, $T_b = 18.5$ °C, and acclimation to B) 22 °C, C) 22 °C and D) 24 °C. Probability of local population persistence is coded blue (1.0) and extinction is coded red (0.0). Islands of blue color (persistence) are located at high-elevation sites (denoted by grey scale), where we propose assisted migration sites.

negative effect on *A. tigrinum*, that was projected to go extinct (Fig. 3C–D). Finally, a change in forest cover in the current range of *A. mavortium stebbinsi* did not alter the probability of persistence.

3.4. Assisted migration

To illustrate the climate warming impacts on high elevation refugia, we present maps of extinction risk for *G. morafkai* showing a few high elevation refugia in 2070 (logistic regression of extinction risk and

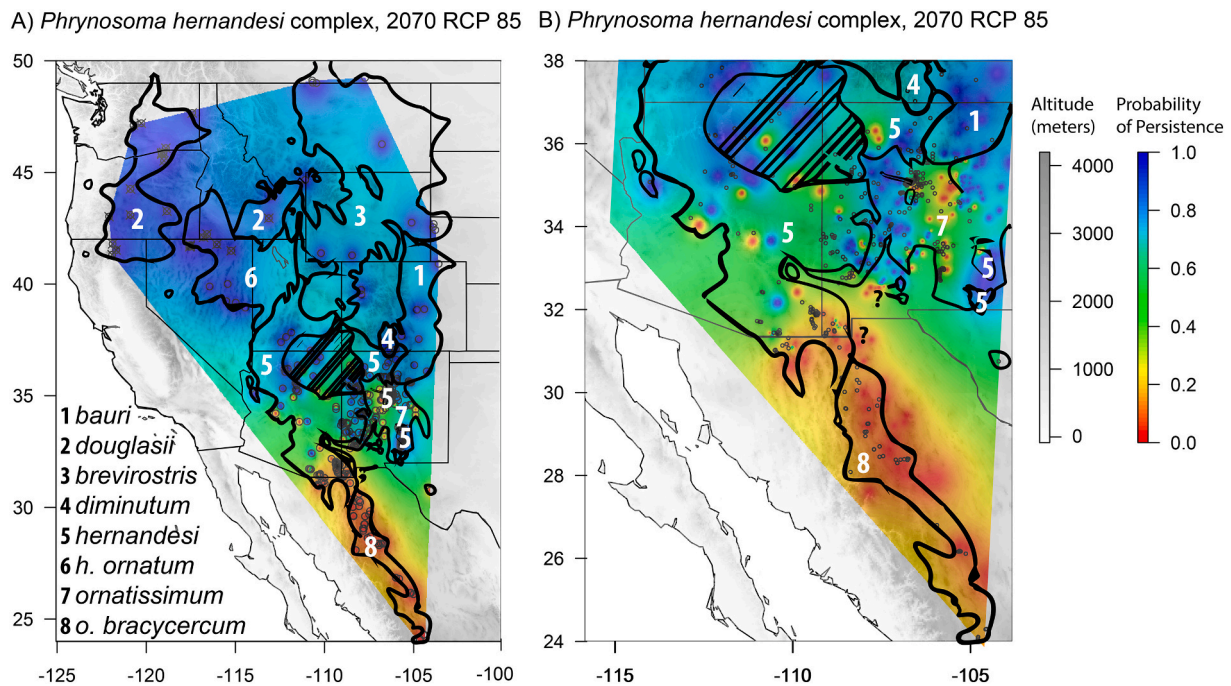


Fig. 6. Extinction risk for species in the A) *Phrynosoma hernandesi*-*douglasii* complex (species labeled 1–8, legend in panel A, hashed lines denote a hybrid zone) under scenario 2070 RCP 85. B) Higher resolution map for those species at greatest risk extinction and in New Mexico (*P. ornatissimum*) and México (*P. ornatissimum brachycercum*).

elevation; Fig. 4B, 2070 RCP 45: $\chi^2 = 19.97$, $P < 0.0001$; Fig. 4E, 2070 RCP 85: $\chi^2 = 5.14$, $P < 0.01$). Climate refugia for *G. morafkai* are spatially separated in the 2070 RCP 85 scenario and are surrounded by low elevation habitats that have low persistence probabilities. The spatial separation of the refugia with low quality interstitial habitat eliminates the potential for migration corridors that might sustain gene flow and in turn exacerbating extinction risks due to the small size of each climate refuge (Fig. 4F). Under a 2070 RCP 45 scenario for *G. morafkai*, low-elevation migration corridors are present (4D). Given the network of protected areas on Federal Lands in the southwestern U. S. (e.g., Grand Canyon Parashant National Monument, northern Arizona and Coronado National Forest, southeast Arizona) and Biosphere Reserves in México (Fig. 4C), the species is at low risk overall. Most of the climate refugia for *G. morafkai* under the 2070 RCP 85 scenario include protected areas where the species might persist in the U.S. The new assisted migration sites that we propose (Fig. 4F) are at extralimital margins in the east (eastern Arizona) and north (southwestern Utah) of the contemporary distribution. Establishing such new “reserves” would greatly enhance connectivity along the eastern margin.

3.5. Assisted migration and acclimation capacity

For *Ambystoma mavortium stebbinsi*, we illustrate the potential for assisted migration to high-elevation sites as a potential rescue from extinction (Fig. 5A). Assuming its estimated T_b of 18.5 °C, only a few sites at high elevation would persist under climate warming. However, if this salamander species could raise its T_b to higher values of 20 °C and 22 °C through acclimation (Fig. 5B and C), it could persist at all assisted migration sites we propose. If it raised its T_b to 24 °C by acclimation, it could persist at all known contemporary locations, as well as all assisted migration sites. An increase in T_b 's of 2–4 °C through acclimation are typical for the parental species of *A. m. stebbinsi* (*A. m. nebulosum* and *A. m. mavortium*) and require acclimation to temperatures ranging from 5 to 20 °C. Unfortunately, few estimates of acclimation to temperatures higher than 24 °C are available.

3.6. Case study for management strategies under climate change: assisted migration

A key question remains to be addressed under assisted migration, are sites going to be suitable for both the warm and cool limits that set a species' distribution? A schematic of site selection process in the face of cool and warm ecophysiological limits is given in Fig. 8.

In analyses of extinction risk under warming, we used the 95 % quantile to compute the critical hours of restriction that limit habitat suitability in the face of heat stressors. However, assisted migration sites should enable access to activity with sufficient hours above the voluntary lower T_b limit for activity, foraging, reproduction and growth. We computed hours of activity for *G. morafkai* (derived from 5 % quantile of h_a values, Fig. 8) at contemporary sites, and compared this to the hours of activity at transplant sites in 2070. The distributions were not significantly different (contemporary: 10.4 h/d, 2070: 9.6 h/d in future 2070 assisted migration sites, $t = 0.59$, $P > 0.55$), and proposed assisted migration sites in 2070 had a similar 5 % quantile for hours of activity in contemporary conditions (9.3 h/d vs. 8.9 h/d for contemporary and assisted migration sites respectively, during the reproductive period defined above). Thus, proposed assisted migration sites by 2070 would be suitable for both the hot and cool eco-physiological limits that define the species ranges: consequently, these should be suitable sites.

As noted above for tortoises, assisted migration sites for salamanders should enable access to activity above the minimum voluntary lower T_b such that there are sufficient hours for foraging, growth and reproduction. Hours of activity at contemporary versus assisted-migration sites in 2070 were not significantly different (contemporary: 6.6 h/d, 2070: 6.4 h/d in future 2070 assisted-migration sites, $t = 0.59$, $P > 0.55$), suggesting that assisted-migration sites should become physiologically suitable for transplantation (by humans) at least by 2070.

4. Discussion

The predicted threshold of complete protection from climate-forced extinction in high elevation refuges (averaged across species) is relevant

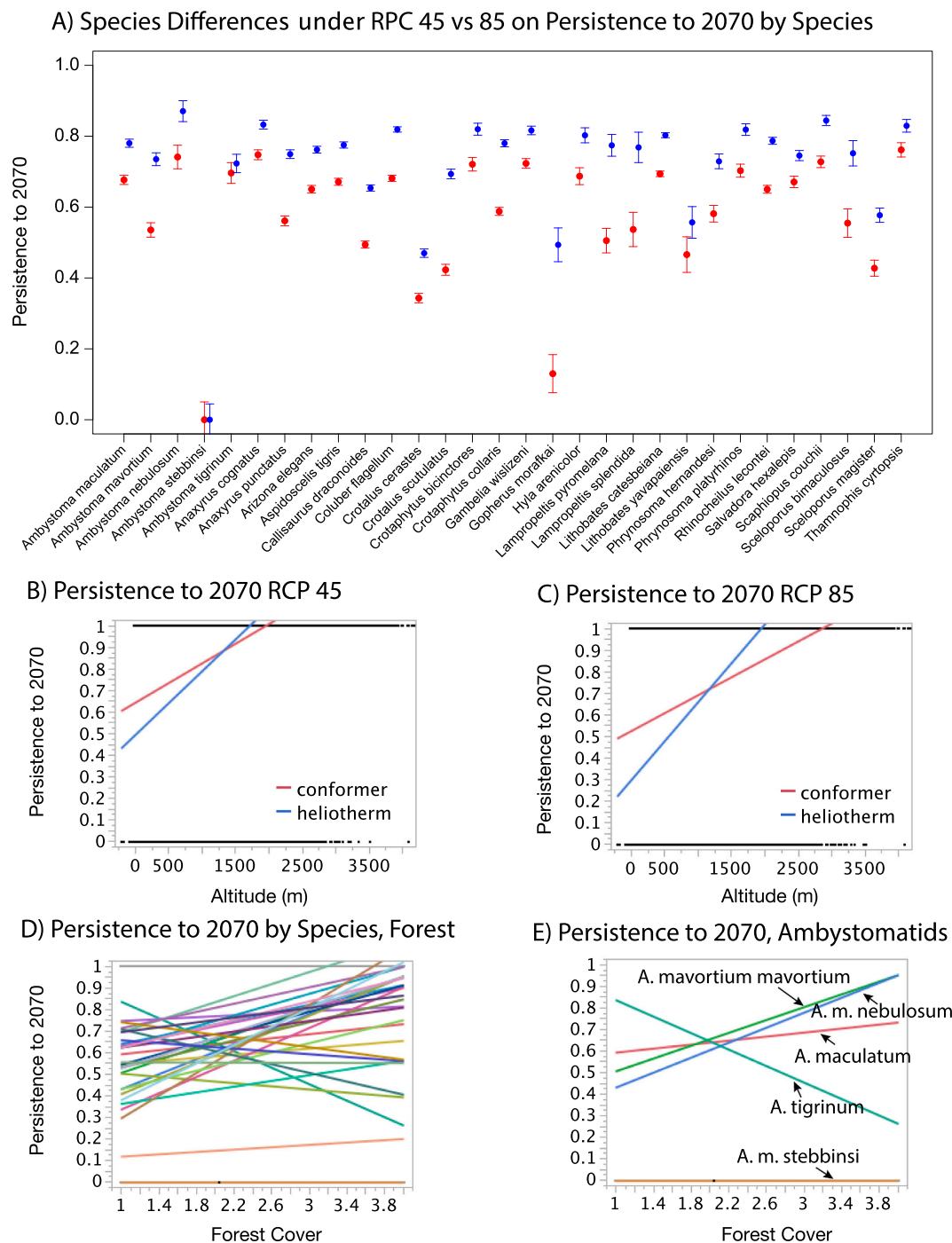


Fig. 7. Persistence to 2070 (probability of one) or extinction (probability of zero) of local populations (mean $\pm$ SE) (coded blue for RCP 45 and red for RCP 85 scenarios) as a function of A) species and B) covariates for Altitude (m) for 2070 RCP 45 and C) 2070 RCP 85, partitioned by heliotherms (blue line) and conformers (red line).

for resource managers, because most national parks, national forests and biosphere reserves already include montane habitats. In the RCP 85 scenario for 2070, heliotherms and conformers obtain protection at high elevation sites (Fig. 7B). Furthermore, the risk of extinction for thermal conformers is lower than for heliotherms at lower elevations. The difference in probability of persistence to 2070 at sea level (elevation = 0 m) varies from 0.53 to 0.27 under RCP 85 for conformers and heliotherms, respectively. The nocturnal behavior of conformers likely contributes to the lower extinction risk they experience at lower elevation. Nocturnal lizard families of the world (e.g., Gekkota) also have a low extinction risk under climate warming (see Table 1, Kearney and

Predavec, 2000; Sinervo et al., 2010).

The impact of forested habitat on reduced extinction risk was uniform across both modes of thermoregulation, with probability of persistence to 2070 under RCP 85 climbing from 0.6 in non-forested habitats up to 0.8 in completely forested habitats (Fig. 7C). Some taxa can obtain complete protection in nearly intact forest habitats. For example, among the ambystomatid salamanders studied here, *A. mavortium nebulosum* and *A. mavortium mavortium* in forests obtain near complete protection from climate change (Fig. 7E). The protective effect of forests is likely driven by the less rapid velocity of climate warming in forested compared to unforested habitats. Nevertheless, the

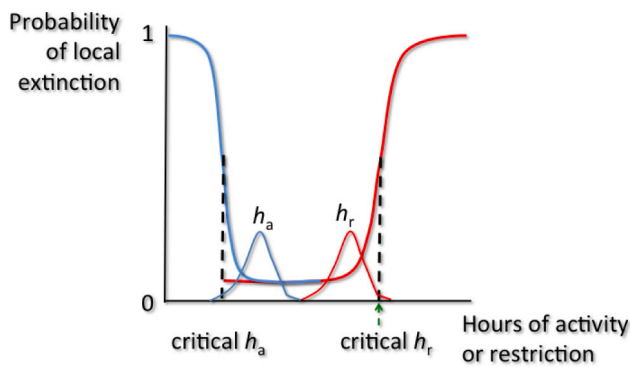


Fig. 8. A schematic for site selection based on the dual criteria of upper (in red color) and lower limits (in blue) for normal activity. The current distribution of h_r values, hours of restriction (e.g., $T_e < T_b$ observed in the species), and h_a values, hours of activity (e.g., $T_e > \text{lower voluntary } T_b$ observed in the species) as related to probability of local extinction for upper and lower limits (sigmoidal red and blue lines). Suitable sites for assisted migration in future time periods should be within these “normal” eco-physiological limits as defined by the species distribution in the contemporary period.

impact of forests can be complex depending on season (see Bonan, 2008), as evidenced by seasonal climate surface projections that downscale weather station data to smaller spatial scales (Fick and Hijmans, 2017). The climate surface parameters (daily maximum and minimum temperature, $T_{\min}$ and $T_{\max}$) we used in our models likely capture these complex effects in extinction risk calculations. Causes of extinction risk associated with level of forest cover were species-specific (Fig. 7D). This pattern will require experimental validation involving forest manipulation studies at landscape scales coupled with ground-truthing, as is currently being conducted in the Atlantic Forest of Brazil (Brancalion et al., 2013; Melo et al., 2013). In addition, experimental studies of impacts of vegetation on behavioral thermoregulation will also enhance our understanding of the eco-physiological responses of ectotherms (Sears et al., 2016).

These general findings of protection afforded by elevation and from forest cover have implications for extinction risk of conformers versus heliotherms, and implications for management strategies of extinction risk in desert-endemic herpetofauna. A targeted set of biosphere reserves and new National Parks, or other types of protected areas, such as wilderness areas or National Monuments, that are adjacent to at-risk species and focused on montane and forested ecosystems in the arid southwest could potentially increase species persistence of all taxa regardless of whether they are conformers or heliotherms. However, each species will have its own threshold depending on its thermal physiological traits and microhabitat requirements, such as forest cover. Below we illustrate these mitigation strategies in a species at gravest risk of extinction under climate warming, *Ambystoma mavortium stebbinsi*. Also, we consider specific implications of our findings for developing conservation strategies to ameliorate impacts of climate change.

4.1. Management strategies under climate change: assisted migration and latent acclimation

The Sonoran Desert Tiger Salamander, *Ambystoma mavortium stebbinsi*, is federally listed as endangered in the U.S. (Hossack et al., 2016). The distribution of the salamander is in southern Arizona (San Rafael Valley) and Sonora Mexico (Hossack et al., 2016). Two mountain ranges border the San Rafael Valley in Arizona (Huachuca and Patagonia Mountains) and another in northern Mexico (Sierra de San Antonio). Analyses of all contemporary locations indicate that none of these sites across its very limited geographic range will be climatically suitable by 2070 (Fig. 5A). Specifically, all populations are predicted to go extinct regardless of RCP 45 or RCP 85 scenario (Figs. 3C, D, 5A). Nevertheless,

a simple assisted migration can be implemented by using transplant sites in adjacent mountain ranges and other public lands in Mexico that surround the current range of this amphibian (see below; Fig. 5A–D).

Ambystoma mavortium stebbinsi is thought to be a hybrid species, produced when *A. m. mavortium* and *A. m. nebulosum* hybridized during a cooler and wetter epoch (Jones et al., 1995). Habitat preferences of the two ancestors are useful in assessing habitat for assisted migration sites. Both parental species occur in forested and montane habitats and both gain protection at such sites (Figs. 4C–D, 7E). While *A. m. stebbinsi* is not currently found in ponds within forested areas, montane areas adjacent to its current distribution are forested and thus, it could gain a climate refuge in open, forested and montane sites given the availability of suitable aquatic habitats (e.g., within the Coronado National Forest in the Huachuca Mountains to the east, Patagonia Mountains to the west, Canelo Hills to the north, and similar montane sites in northern Mexico, Fig. 5). We suspect that it does not occur in these areas today, simply because the mountainous terrain with high rates of erosion does not support ponds needed for breeding and larval development.

4.2. Translocation strategies

The successful translocations of *G. agassizii* within California (Drake et al., 2012; Nussear et al., 2012) and of *G. flavimarginatus* to New Mexico (Hansen et al., 2010), provides support for the conclusions of our model regarding assisted migration. However, other studies suggest that translocation has a checkered history of success for two species of desert tortoises (Germano and Bishop, 2009; Germano et al., 2015; Sullivan et al. 2015) suggesting that more research is needed to improve results (e.g., Germano et al., 2017). Although assisted migration and translocation are similar, they are not the same. The former provides corridors for dispersal and depends on the intrinsic dispersal behaviors of the species. In contrast, translocation depends on humans to move the species. We think this distinction is important, because while we propose translocation at the transplant sites, we assume the tortoise will ultimately expand across the newly suitable habitat. Other barriers such as highways and other human barriers may limit this outcome. Thus, while translocation to transplant sites seems a promising and perhaps a necessary vehicle for tortoise survival, it must be considered in the “matrix” of our human-altered landscapes. We could initiate such translocations and transplants by assessing diverse protected sites projected to be suitable in 2020 and 2050. In subsequent years, we could then apply a leapfrog approach and move them again from 2050 to 2070, based on a careful consideration of other obstacles impinging their ultimate dispersal. But management plans must protect those potential transplant sites.

4.3. Thermal acclimation as an escape from climate warming

Additional studies of thermal physiology (especially of capacities for evolution and for acclimation) will be required to generate a comprehensive assessment of extinction risk and provide more robust eco-physiological inferences. In previous analyses of extinction risk, we assumed that the thermal physiology of most ectotherm species is static, given that heritability for thermal preference is too low to respond rapidly enough under climate warming (Paranjpe et al., 2013; Sinervo, 1990; Sinervo et al., 2010; Logan et al., 2018). In modeling extinction risk for *A. m. stebbinsi*, we considered a potential acclimation strategy that might mitigate future climate warming. Some species of ambystomatid salamanders can acclimate to higher temperature and the magnitude of these plastic responses is considerable.

For example, Jefferson’s salamander (*Ambystoma jeffersonianum*), a species with a northern distribution, can increase its $CT_{\max}$ by approximately 1.5–2 °C when acclimated at 5, 15 and 25 °C; the acclimation capacity of other amphibians can be much higher (Rohr et al., 2018). In addition, the capacity for acclimation in thermal preference is 2–4 °C in *Ambystoma maculatum* and *A. texanum*, which have a more southern

distribution than *A. jeffersonianum*. Acclimating capacity in CT_{max} is 3–4 °C in *A. maculatum*, *A. texanum* and *A. opacum* (Keen and Schroeder, 1975). Delson and Whitford (1973) demonstrated both local adaption and differences in acclimation capacity of CT_{max} of 2–3 °C, when reared at 10 versus 20 °C, in montane versus lowland *Ambystoma mavortium mavortium*, one of the parental species of the hybrid species *A. m. stebbinsi*. Heath (1975) likewise demonstrated altitudinal variation in thermal preference and acclimation capacity of 2–3 °C of *A. mavortium nebulosum*, the other parental species of *A. m. stebbinsi*.

Therefore, if *Ambystoma mavortium stebbinsi* exhibits similar acclimation capacity as its ancestral parental species, it might already possess a latent ability to escape extinction. If *A. m. stebbinsi* could elevate its thermal preference from 18.5 °C to 22 °C through plasticity, it could persist at all proposed transplant sites and could also persist at few of the higher elevation contemporary sites (Fig. 5C). If it could increase its thermal preference to 24 °C (~4.5 °C) it could persist across all known locations and rescue itself (Fig. 5D).

The empirical study of acclimation capacity is critical because *A. m. stebbinsi* exhibits lower levels of genetic variation compared to *A. m. mavortium* and *A. m. nebulosum*, and may also exhibit low heritability (Jones et al., 1995). Furthermore, *A. m. stebbinsi* exhibits a lower frequency of cannibal morphs than does its closest congeners (Hossack et al., 2016), perhaps indicative of either depleted additive genetic variation, or reduced plasticity (Pfennig et al., 2002). On the other hand, newly formed hybrids between *A. californiense* and the invasive *A. mavortium mavortium*, exhibit “hybrid vigor” in thermal performance curves. In particular, F₁ hybrids have higher performance than either parental type (Johnson et al., 2010) suggesting that the older hybrid species *A. m. stebbinsi* might harbor similar hybrid vigor. In this regard, studies of acclimation plasticity in *A. m. stebbinsi* across its range would facilitate more reliable inferences on ecophysiological risks of extinction. Moreover, we could identify preferred pond populations where plasticity is prevalent compared to other populations that lack the propensity for plasticity. Pond populations harboring genotypes with greater plasticity might be more likely to survive translocations. We suggest the need to identify genotypes from such ponds to enhance the success of translocation activities. Future models should also include other vulnerable amphibian life cycle stages including egg, larval stages. Another physiological trait to include in mechanistic models is the resistance to drying events of terrestrial stages in amphibians, as well as egg and juvenile stages of reptiles.

Hybridization is an additional concern for managing species vulnerable to climate warming and drying. As an example, *A. m. mavortium* is a non-native invasive species that hybridizes with native species in several cases (Hossack et al., 2016): *A. m. mavortium*, threatens *A. m. stebbinsi* in Arizona (Storfer et al., 2004), and *A. m. mavortium* threatens *A. californiense* in California, and hybrids are spreading rapidly (Fitzpatrick and Shaffer, 2007).

The presence of congeneric species in suitable montane habitat refugia is also a major factor to consider when planning for assisted migration or translocation activities. Developing conservation measures that mitigate the effects of species interactions (e.g., interspecific competition) now is clearly warranted, particularly in the case of species complexes such as *Phrynosoma hernandesi*. In this species complex, a low-elevation species (*P. o. ornatissimum*) faces extirpation from climate change in New Mexico as does *P. o. brachycercum* in Mexico. However, in both species adjacent montane habitat refugia are already occupied by *P. hernandesi*. The ability of lower elevation species to colonize montane habitats may be hampered by the exclusion of suitable thermal microhabitats by the montane species. In salamanders, invasive *A. mavortium mavortium* hybridizing with native *A. mavortium stebbinsi* (see above) merits considering the appropriate thermal habitat for the vulnerable species. Conservation planning that involves a species complex presents a challenge for reserve managers. Constituent species in an evolving complex are likely to have similar thermal niches; contact zones delimiting species may rapidly shift over the next decades of climate

warming blurring the capacity of reserves to serve as a refuge for the species. In this regard, we have observed rapid geographic shifts in other species complexes in México, such as in the species complex of *Sceloporus anahuacus*, *S. palaciosi*, and *S. grammicus* on the Ajusco volcano (Sinervo et al., 2010). Therefore, hybrid zones may be particularly vulnerable to perturbation by climate change. Loss of such evolutionary information and unique genetic diversity in hybrid zones presents a pressing and unique challenge for conservation biology.

CRedit authorship contribution statement

Barry Sinervo: Conceptualization, Methodology, Formal analysis, Funding acquisition, Supervision. **Rafael A. Lara Reséndiz:** Investigation, Writing – review & editing. **Donald B. Miles:** Conceptualization, Investigation, Funding acquisition, Writing – review & editing. **Jeffrey E. Lovich:** Investigation, Resources, Writing – review & editing. **Philip C. Rosen:** Investigation, Resources, Writing – review & editing. **Héctor Gadsden:** Investigation, Writing – review & editing. **Gamaliel Castañada Gaytán:** Investigation, Writing – review & editing. **Patricia Galina Tessaro:** Investigation, Writing – review & editing. **Víctor H. Luja:** Investigation, Writing – review & editing. **Raymond B. Huey:** Investigation, Writing – review & editing. **Amy Whipple:** Investigation, Writing – review & editing, Funding acquisition. **Víctor Sánchez Cordeiro:** Investigation, Writing – review & editing. **Jason B. Rohr:** Conceptualization, Investigation, Writing – review & editing. **Gabriel Caetano:** Software, Methodology, Writing – review & editing. **Juan C. Santos:** Software, Methodology, Writing – review & editing. **Jack W. Sites:** Investigation, Writing – review & editing. **Fausto R. Méndez de la Cruz:** Conceptualization, Investigation, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data, proofed occurrence records, maps of extinction risk, and R code will be deposited in [10.6084/m9.figshare.24549505](https://doi.org/10.6084/m9.figshare.24549505). Thus, extinction risk of specific taxa at known locations can be further analyzed by land managers in planning new preserves.

Acknowledgements

We thank the three anonymous reviewers for their constructive comments and suggestions on a previous version of the manuscript.

Funding

This project was supported by a grant from the United States Fish and Wildlife Service under the DLCC program (BS, PCR, DBM and JL); a NSF Emerging Frontiers Grant (EF-1241848, BS, DBM, and JWS Jr); NSF DEB (1950636, DBM); NSF (IOS-1038016, RBH); NSF (DEB-2016372, JCS); UC MEXUS-CONACYT CN-17-129 (685-IB) to BS and FRMC; UC MEXUS, CONAHCyT, and PROFABI-ITSON (2023.033RALR) to RALR; PAPIIT-UNAM IN212119 and PASPA-DGAPA CJIC/CTIC/0781/2022 to FRMC; BS and AW were supported by a FSML grant from NSF. JEL was supported by a grant from the California Energy Commission, Public Interest Energy Research (PIER) Program. BS was also supported by ISEECI, the Institute for the Study of the Ecological and Evolutionary Climate Impacts, which is funded by a UC President Research Catalyst Award, University of California, Office of the President; TNC and BLM funding; and by the UC President’s Mexico Climate Change Initiative. Any use of trade, firm, or product names is for descriptive purposes only

and does not imply endorsement by the U.S. Government.

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