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Climate Change and Collapsing Thermal Niches of Mexican Endemic Reptiles

White Paper for the Environmental Working Group of the UC-Mexico Initiative

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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 due to extinction. Climate models predict dramatic extinctions and distributional shifts in the next century, but there are few ground-truths of these dire forecasts leading to uncertainty in predicting extinctions due to climate change. Previously, we reported on recent extinctions of Mexican *Sceloporus* lizards by comparing recent surveys to historical distributional records for 48 species at 200 sites. We also ground-truthed extinctions on five continents across 8 lizard families by comparing observed and predicted extinctions from an eco-physiological species distribution model and obtained a high R^2 of 0.72 (*1, 2*). Here, we derive more detailed predictions for 15 terrestrial reptile families and 142 species for the Mexican and California Biogeographic provinces using all known museum occurrence records, and detailed measures on eco-physiology. We adopt the eco-physiological model of extinction developed earlier but use a species-specific model. We predict massive and rapid extinctions of 22% of the reptile populations in Mexico within the next 50 years. We also predict that 3 of 15 reptile families, all three endemic to the Mexican and Californian biogeographic provinces, will go extinct by 2070, the hallmark of the beginnings of a mass extinction event. However, extinctions may be attenuated by forest cover and by presence of montane environments in contemporary ranges. We describe impacts of altitude on three species (*Gopherus morafkai*, *G. evgoodei*, and *Gambelia sila*) to illustrate regional management strategies (AZ-Mexico, Sinoloa, CA) for reserves in tandem with global strategies of CO_2 limits that might limit climate impacts. By carefully selecting new montane preserves adjacent to desert and tropical forest habitats, and by implementing global controls on atmospheric CO_2 emissions, extinctions may be reduced to less than 11% of species and only a single reptile family.

Introduction

Global climate change is a pervasive threat to plants and animals in nearly all biomes and ecosystems. 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 adapt to the new local environments either by plasticity or adaptive evolutionary responses. The third and final response is failure to adapt and extinction of local populations or entire species. Whereas there is evidence of climate change affecting species range limits in a limited set of taxa (*3, 4*), evidence of extinctions due to anthropogenic climate change (*5-7*) at a global scale across continents is limited. In addition, most current forecasting models (*8, 9*) are not calibrated with actual extinctions (*10*), but rather models are based on predicted effects of thermal physiology on demographic variables, and predictions of ensuing demographic change on local population extinction probabilities. Alternatively, models are based on range shifts or species-area relationships (*11*), or more elaborate mechanistic models incorporating the role of thermal adaptations (*12*). These issues have generated considerable debate as to the expected magnitude of extinctions (*12*). Empirical validation of biotic impacts of climate requires evidence that observed extinctions are tied to macroclimate events and explicit ground-truth studies of microclimate effects linked to demographic processes (*13*). Furthermore, linking extinction to changing thermal regimes [e.g., biophysical thermal cause (*14*)] requires demonstration that thermal physiology (*12*) is compromised by the pace of current climate

change because rates of evolution lag the pace of climate change (*15*) due to constraints on the genetic architecture of thermal adaptations (*16*).

Here, we assemble a large database of occurrence records (N=22981) of Mexican endemic and widespread species (N=142) obtained from museum records (Figure 1). We present a model that addresses critiques (*12, 17*) regarding predictions because our estimates are based on a model ground-truthed against observed and predicted extinctions (*2*) as governed by the mechanisms of thermal physiology and behavioral thermoregulation (*1*), traits that exhibit low heritability and thus cannot respond rapidly by selection due to climate change (*1, 18, 19*). We then extend the model to endemics and widespread species of Mexico, Arizona, and California and show that a global climate crisis of unprecedented proportions is impacting reptilian lizard families and will devastate biodiversity by 2070 unless dramatic steps are taken at global scales to reduce carbon emissions and at a regional scale within Mexico to develop new reserves. In this regard, we assemble data on altitude and level of forest cover for all geo-referenced locations and analyze geographic factors that ameliorate extinction risk. We converted published forest layers to a scale representative of level of forestation: ocean = N.A., 0 = water, 1 = other land cover, 2 = other wooded land, 3 = open or fragmented forest, and 4 = closed forest (*20*). For climate layers, we used the MPI-ESM-LR (Max Planck Institute Earth System Model) at 1.8758 degrees resolution (downscaled to 1 x 1 km grid cells) under 2 models of Representative Concentration Pathways (RCPs) assuming +4.5, and +8.5 W/m^2, 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. This ensemble of models captures observed patterns of temperature and precipitation during the control period (*21*) and thus may be better able to predict future climate change.

For all climate surfaces, geographic covariates, and species occurrence records (Figure 1C), we used a spatial extent of longitude = [-125°, -75°], latitude = [5°, 40°] to span the occurrence records of the chosen taxa, and at a grid size of 30 arc-seconds (~1 km × 1 km). We specifically excluded several widespread species that range from México to the northern U.S. and Canada (i.e., beyond the spatial extent used here) such that we can focus our analysis on desert and neotropical species of Mexican and Californian Biogeographic Provinces. The full analysis of North American and Central American species will be presented elsewhere.

We used records of body temperature and thermal preference data published in Sinervo *et al.* (*1*) on 51 species and assembled new data from our field research in Mexico and the U.S. during 2010 to 2015 on 91 other species in reptile families Anguidae, Annielliidae, Bipedidae, Corytophanidae, Crotaphytidae, Dibamidae, Helodermatidae, Iguanidae, Phrynosomatidae, Polychrotidae (now Dactyloidae), Scincoidae (a superfamily with 2 families analyzed, Scincidae and Scincomorpha), Teiidae, Xantusidae, and Xenosauridae, all lizard families, as well as 5 species of tortoise in the Testudinae. The final data set consists of 142 species in Mexico and California in 15 reptile families, along with a few species in a given family just outside of the study region, to give us power to compute extinction risk across the families that occur in the Mexican and Californian Biogeographic Provinces (e.g., *Cricosaura typica* in Cuba in the Xantusidae [and a few other Caribbean taxa], the fossorial species *Neoseps reynoldsi* in the Scincidae, along with *Gopherus polyphemus* in the Testudinae and *Sceloporus woodi* in Florida in the Phrynosomatidae). We targeted a Californian species because of concern about their conservation status including *Gambelia sila* in the Crotaphytidae, *Uma inornata* in the Phrynosomatidae, and 5 species in the Anniellidae to estimate family level extinction for the Mexican endemic *Anniella geronimensis* of Baja. Thus, our analysis spans the neotropics beyond Mexico (e.g., FL, Cuba) along with desert ecosystems in the US (CA) and Mexico. Finally, many

Mexican species have northern ranges that reach Arizona, New Mexico and Texas, so we also included these taxa and regions in our analysis.

Some reptiles are heliotherms that bask and require exposure to solar radiation to attain physiologically active body temperatures (22-25), while other reptiles are conformers that live in forests where thermoregulation opportunities (e.g., basking) are so limited that they conform to ambient temperatures. In both types of reptiles, activity during hot weather could lead to body temperatures (T_b) exceeding their critical thermal maximum (CT_{max}) and result in death. In localities or seasons where ambient temperature (T_a) exceeds CT_{max}, reptiles retreat to thermal refugia rather than risk death by overheating. However, longer time intervals spent in retreat sites reduces the time for foraging and hence potentially constrains metabolically costly functions like growth, maintenance and reproduction. We hypothesize that climate change will ultimately trigger demographic collapse culminating in local extinction (1), if the limits of behavioral plasticity in thermoregulation are exceeded and failing a plastic response, limits on the rate of adaptation are exceeded (1, 18, 19). For example, analysis of a Mexican lizard species (*Sceloporus mucronatus*) during a severe warm spell demonstrates that cessation of reproduction in 1998 may have been the catalyst, which precipitated extinctions in several adjacent populations (2).

To develop geographic and climate predictors of extinction risk, we analyzed extinction risk with regression (e.g., predicted to be extinct = 0 vs. persistent = 1), ignoring phylogeny, but including geographical covariates. We will treat phylogenetic effects (*26, 27*)] in a companion paper. Effects detected at the level of species based on the full data set were also significant in extinction analyses involving phylogenetic analyses. Analysis of occurrence records in a geographic framework is useful information for land managers that can target specific populations and species (at risk of extinction) with proactive delineation of new Biosphere Preserves or National Parks, as a function of the geographical covariates of altitude and forest cover (Fig. 1AB). All data and R code will be deposited in the University of California Merritt Repository such that extinction risk of specific taxa at known locations can be further analyzed by land managers in planning new preserves.

In analyses presented here, we adopted a multivariate analysis of repeated measures analysis of variance of extinction risk, comparing different climate scenarios of 2070 under RCP 85 versus 2070 under RCP 45, using geographic covariates altitude, forest cover, factors for thermoregulatory mode (conformer vs. heliotherm) and family. We considered a given species at risk of total extinction across its range (for a given climate scenario) if the P-value on probability of extinction across all occurrence records was ≤ 0.05. Similarly, we considered a family at risk of total extinction if the P-value for average species persistence in the family averaged ≤ 0.05.

Data on species physiology of Mexican reptiles and known occurrence records, when merged with eco-physiology in our model, hypothesizes that each species is optimally adapted to its local thermal habitats (at sites where it historically occurred before climate change), and that non-random extinctions will be will be concentrated at warmer range boundaries, or where the velocity of climate change is most rapid, where taxa are limited either by thermal physiology or species interactions, e.g., competition, predation (*28, 29*). We specifically included mode of thermoregulation as a factor (heliotherm vs. conformer) because we hypothesized a priori that conforming reptiles would be at greater risk of climate-change induced extinctions, given that previous theory and data indicates that tropical conformers are closer to their thermal limits because they are adapted to life in the cooler habitats afforded by closed forest canopies (*30*). In

addition, recent manipulations of vegetation cover indicate an ameliorative effect on physiology and behavioral thermoregulation in the context of warming temperatures (*31*).

In analysis of eco-physiology, we measured operative environmental temperatures (T_e) using physical models (*32*) deployed at 200+ sites across Mexican tropical forests in the Yucatan, the Transvolcanic region of central Mexico, the Sierra Madre Orientale and Occidentale, the Sonoran, Chihuahuan, Mojave, and San Joaquin Deserts, as well as in Tropical Dry Forests and Desert Thorn Scrub habitats that are transitional in Sonora and Sinaloa. The full analysis of T_e data will be presented elsewhere, but here we use a robust set of four non-linear regression models developed for reptiles of various size and tortoises spanning tropical forests and deserts sites (N = 40 sites) relating hours of restriction in activity to air temperature [daily maximum (T_{max}) and minimum (T_{min}) air temperature) and evolved physiology (field T_b and/or T_{pref} as measured in a laboratory thermal gradient). Figure 2 presents fitted curves for species of *Gopherus* in the family Testudinae in the desert and tropical deciduous forest habitat.

Depending on presence of lizard families of different sizes in a local habitat, we deployed (data loggers, Onset Computer) small (10×12.5 cm) and medium PVC models (15×2.5 mm) suitable for computing constraints of hours of restriction on small and medium-sized lizards in the Phrynosomatidae (2), 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 families Crotaphytidae and Iguanidae. For select species such as *Heloderma suspectum,* which might use a combination of conforming, heliothermy and thermal inertia strategies of behavioral regulation, we deployed larger models (45×8 cm), painted with natural colors and patterns. In select conforming species such as those in the Corytophanidae, Polychrotidae, Scincidae, and Anguidae, we also deployed Te models in forested habitats to confirm thermoregulatory mode. For fossorial taxa, such as the Bipedidae, we deployed temperature data loggers (ibuttons) at various depths to register thermal profile of soils. For other conformers in the Xantusidae and Xenosauridae, we placed data loggers in natural sites used during activity. Finally, 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 Thorn Scrub and Tropical Deciduous Habitats, where different modes of thermoregulation are exhibited (e.g., *G. morafkai* of the DTS is a heliotherm and *G. evgoodei* of the TDF is a conformer). Data analysis of T_e models confirmed that a simple set of robust non-linear regression models (four in total) relating hours of restriction to the key climate variable T_{max} and physiological parameter, preferred body temperature in a laboratory thermal gradient, T_{pref} or field T_b. The full data set reflects the largest T_e data set yet assembled and spans most habitats of all reptile families we consider here. An example of these curves analyzed for hours of restriction and hours of permissible activity is presented in Figure 2, using data analyzed from Zimmermann et al. (*33*) on the desert tortoise, *Gopherus agassizii*.

Dramatic climate warming during winter and spring months should have profound effects on reptiles because these periods are critical for reproduction. For viviparous and oviparous reptiles of Mexico, we hypothesized that warm spells during April through June would be critical months that could affect gestation time, reproduction date, post-parturition survival of neonates and female parents. These months are also critical for heliotherms that might produce one to three clutches during April-June. Furthermore, viviparous conformers give birth near the end of May-July, across the geographic study region based on a review of reptile reproduction in Mexican reptiles (34-42). Thus, for our study region, reptiles tend to breed in the same season across a large geographic area. Our model thus incorporates eco-physiological and phenological

effects in the form of the *initiation* and *cessation* of breeding activities. Functions for behavioral thermoregulation as constrained by ambient temperature have *periodic functional forms* (sinusoidal in the case of T_{min} to T_{max} from night to day for conformers, or numerically integrated from the raw data collected on dataloggers for heliotherms). The data can be converted to hours of restriction or activity (Fig. 2), which when regressed on (T_{max}-T_{pref}) yield sigmoidal functions (Fig. 3). These are very general ideas of phenology referred to in plant studies as degree-day time scales. However, when couched in terms of time for activity or of temperature physiology, they are best thought of as *physiological time scales* (43), integrated across the day and night and year, which can be coupled to extinction risk models.

A global model of extinction risk for lizards applied to Mexican reptile biodiversity

The utility of the extinction model of eco-physiology is reflected in the simple set of parameters used to predict extinction risk. A climate change surface is required. Contemporary (1975, worlclim.org) and future climate surfaces (2050, 2070, RCP 45 and 85) can be used to predict T_{max} at any geographic coordinate in México at any point in the future and thus can be used to predict impacts on extinction risk. For heliothermic reptiles, we used the same model, ground-truthed for the lizards of Mexico; if their restriction in activity while basking exceeded the species-specific critical hours of restriction h/d (44-46), based on the non-linear equation relating $T_{max} – T_b$, we assumed they would go extinct at that sites. We adopted a conservative measure of the critical hours of restriction within each species using a similar $P \leq 0.05$ as used for the previously published for lizard families (1). We computed the critical hours of restriction from the upper 95% quantile of hours of restriction computed across all sites for a given species during the contemporary period of climate (e.g., 1975) [see (44) for a detailed explanation]. If a species at a given site was predicted to exceed this critical hours of restriction we assumed it would go extinct, and if a species was predicted to go extinct across 95% of all known occurrence records we considered it to be at high risk of total species-level extinction. Similarly, if the species within a family were predicted to go extinct across 95% of all known occurrence records within a family we considered it at high risk of total family-level extinction.

Temperature records from the various families of lizards are not just from heliotherms such as lizards in the family Phrynosomatidae, but also from conformers that do not bask but remain very close to ambient air temperature (cycling between T_{min} and T_{max}) (*22*). For both types of reptiles, we averaged all field T_b records with T_{pref} values to obtain one species-specific measure for T_b and T_{pref}, hereafter referred to as T_{pref}. For conformers, we also used the published model for ground-truthed against conforming families (*1*). Conformers are typified by many anolis lizards in the family Polychrotidae, which are common in neotropical habitats. In computing extinction thresholds (critical hours of restriction) for conformers, we do not need to use the relationship between operative model temperatures (e.g., T_e), T_{pref}, and T_{max} to compute the critical threshold for hours of restriction. Conformers are close to T_{air} during the day, if $T_{air} < T_{pref}$, we can compute the hours of restriction in activity as the time that a thermal conformer can be out and active provided that $T_{air} < T_{pref}$. We computed daily excursions in T_{min} to T_{max} climate surfaces (average of April-June T_{min} and T_{max}), as a sine wave for T_{air} with amplitude 24 h. We

coded all species as either heliotherms or conformers based on a review of their published thermal physiology or our observations during collection of the new data used herein. We used the same extinction criteria for conformers as outlined above for heliotherms and histograms for hours of restriction in the Contemporary (1975) from which we derived the critical h_r, and two future climate scenarios (2070 RCP 85 vs 2070 RCP 45) (Fig. 2).

Extinction risk, forests altitude, and thermoregulatory mode

Geographic patterns of extinction risk across all reptile families are presented in Figure 3 for all climate scenarios. Our analysis projects that 20 of 142 species (22%) will be extinct by 2050 under RCP 85, while under RCP 45 only 12 species (8%) will be extinct. Similarly, we project that 31 of 142 species (22%) will be extinct by 2070 under RCP 85, while under RCP 45 only 15 (11%) of species will be extinct under RCP 45. Here we mainly discuss the 2070 scenario (all results found significant for 2070 discussed below were also significant for 2050). Analysis by family (Fig. 4A) suggests that under RCP 85 three families (Annielidae, Bipedidae, Dibamidae) endemic to the Californian and Mexican Biogeographic provinces are projected to go totally extinct by 2070, but under RCP 45 only one (Anniellidae) is projected to go extinct by 2070 (effect of family is significant, for both 2070 and 2050, $F_{14,22963} = 204.49$, P<0.00001, Fig. 4A). All three conforming fossorial families that are predicted to go extinct by 2070 are restricted to low elevation. In contrast, three families of conformers, Anguidae, Xantusidae and Xenosauridae, which are found in diverse habitats (rocks, logs, under debris) in tropical forests and forested, montane habitats, are projected to have the lowest extinction risk among reptile families (Fig. 4A). Finally, families of forest and desert conformers (Corytophanidae, Helodermatidae, Polychrotidae, Scincoidea) are projected to persist nearly as well as heliothermic families (Crotaphytidae, Iguanidae, Phrynosomatidae, Teiidae) under both 2070 RCP 45 and 85. Visual comparison of maps for forests and altitude (Fig. 1BC versus Fig. 3) suggest that climate refuges (region with low extinction) are islands of habitat at high altitude or in regions with forest, which we analyze formally below.

The difference between RCP 45 and 85 for 2070 can be compared with repeated measures ANOVA to isolate families at greatest risk of extinction (2070), and which might benefit from global mitigation strategies involving atmospheric CO_2. We find that there is a significant difference in the degree of amelioration by family, as described above ($F_{14,22966} = 228.15$, P<0.000001). Of the 3 families at greatest risk of extinction, dibamids benefit the most under lower RCP scenarios ($P_{persistence} = 0.0$ vs 0.5 under RCP 85 vs. 45) while annielids benefit the least ($P_{persistence} = 0.01$ vs 0.03 under RCP 85 vs. 45) and Bipedidae was intermediate in this regard ($P_{persistence} = 0.05$ vs 0.13 under RCP 85 vs. 45). The overall amelioration of extinction risk across all families was at a level of P=0.08 between RCP 85 to 45, which in some families predicted to be close to extinction by 2070 represents a substantial degree of protection from climate-forced extinction (c.f., the distance between lines of RCP 45 vs. RCP 95, Fig. 3A).

Patterns of extinction risk of reptile families (and species) were differentially affected by presence of forest cover as a function of heliothermy versus conformity. Heliotherms benefit from forests, while forests exacerbated extinction risk of conformers ($F_{14,22963} = 8.37$, family $\times$ thermoregulatory mode, Fig. 4B, C).

Patterns of extinction risk of lizard families (and species) were uniformly ameliorated by presence of higher elevation montane regions in the contemporary family (and species range), regardless of whether they were conformers or heliotherms. However, amelioration derived from high elevation refugia benefited heliotherms more than conformers ($F_{14,22963} = 8.37$, family × thermoregulatory mode, Fig. 4D, E). This difference in slope between heliotherms and conformers does decrease for the RCP 85 20270 scenario relative to the RCP 45 scenario, which indicates that altitude more similarly affects the two types of reptiles under the more severe climate scenario (lines begin to converge at RCP 85 compared to RCP 45, Figure 3E vs 3D).

The predicted threshold of complete protection from climate change extinction (averaged across families) is of interest for land managers. In the RCP scenario 85 for 2070 heliotherms and conformers obtain near complete protection in climate refuges is obtained above 2500 m (no extinctions are predicted above this altitude, points with 0 persistence = extinct are all below 2600 m). All findings have both general implications for extinction risk of conformers versus heliotherms, and specific implications for potential management strategies of Mexican endemics. We first discuss risk arising from thermoregulatory mode. We first discuss general implications of our findings and then by focusing on three case studies, we discuss the specific implications of our findings for developing conservation strategies to ameliorate impacts of climate change.

Extinction risk of conformers vs. heliotherms

Tewksbury et al. (*9*) conjectured that climate change might have the most dramatic impacts on tropical forms and those that have a low thermal preference, which were hypothesized to have less evolutionary scope for change. Our modeling results indicate conformers with a low T_b such as lizards in the families Anniellidae, Bipedidae, and Dibamidae are at risk of family-level extinction but these are all fossorial conformers, not conformers living in tropical forests. While other conformer families living in tropical forests are not at a grave risk of total extinction, they are at a higher risk of extinction than sympatric heliotherms (e.g., those conformers at high altitude). Thus, our analysis confirms the general hypotheses of higher extinction risk for tropical conformers compared to heliotherms. However, we found that presence of forests (Fig. 1B) accentuated extinction risk of conformers but ameliorated extinction risk of heliotherms in 2050 and in both RCP 45 scenarios, but that under the 2070 RCP 85 scenario the protection afforded by forests to heliotherms erodes. Causes of higher extinction risk for conformers with adjacent forest will require experimental validation involving forest manipulation studies at landscape scales in Mexico as conducted in Brazilian Atlantic Forest (*47, 48*), combined with experimental studies of impacts of vegetation on behavioral thermoregulation of reptiles (*31*). Conformers specifically living in forests appear to exhibit evolved traits that directly impose a greater risk of extinction when they evolve to occupy heavily forested areas. Conversely, conformers evolved to live in relatively unforested areas have evolved physiology and behavior that reduces risk of extinction under climate change. In contrast, heliotherms have evolved a different set of traits when occupying heavily forested areas that reduces risk. A comprehensive Gap Analysis (*49*) would include consideration of forests in reserves and threats from deforestation, which we will consider in another paper.

We also found that species with high altitude refugia in their contemporary distribution would have refugia under climate change and this effect was observed across both heliotherms and conformers. Regardless of the actual cause of the greater risk to conformers in forested

areas, to reduce extinction risk of reptiles in Mexico it is critical to both reduce greenhouse gas emissions and to enhance forestation, but conducting reforestation should be focused on areas where heliotherms are at the greatest risk of extinction. Alternatively, for conformers the presence of refugia at high elevation (altitude uniformly reduces risk of extinction in both modes of thermoregulation), which are forested, may allow them to persist. Thus, a targeted set of biosphere reserves and new National Parks or other type of protected areas, adjacent to at risk species, and focused on desert and tropical forest ecosystems above 2600m could potentially increase species persistence of the most critically at risk taxa. The threshold of 2600 m provides universal protection across all 142 species, but each species will have its own threshold depending on evolved thermal physiology and microhabitat requirements. Here we consider three species to illustrate how reserves might ameliorate extinction risk.

Three case studies for management strategies under climate change

The ultimate aim of these extinction analyses of single taxa is to formulate a plan for the preservation of biodiversity under the threat of climate change using Gap Analysis (*49*), which identifies missing areas of protection for diverse species under threat of extirpation. As a step in this direction, we present three cases studies of species using these extinction criteria for *Gopherus morafkai*, *G. evogoodei* and *Gambelia sila*. For *G. morafkai* and *G. evgoodei* we present the histograms for contemporary climate, from which we derived h_r critical and two future climate scenarios (2070 RPC 45 and 85, Fig. 2), which we used to develop maps of extinction risk under the four climate scenarios of future climate (Fig. 3).

To illustrate the impacts of high-altitude refugia from climate warming, we present maps of extinction risk for *G. morafkai* and *G. evgoodei*, which are both predicted to be protected in high elevation populations. Both species also have climate refugia at higher elevation sites based on logistic regression of extinction risk and altitude (2070 RCP 45: $\chi^2 = 19.97$, $\chi^2 = 5.14$, for *G. morafkai* and *G. evgoodei* respectively, and 2070 RCP 85 $\chi^2 = 19.43$ for *G. morafkai*; too few populations are predicted to survive to compute the logistic regression for *G. evgoodei*). Under RCP 85 the two *Gopherus* species are at differential risk of extinction by 2070. Because *G. evgoodei* ($P_{persistence} = 0.05$) has a persistence probability $P \leq 0.05$ we considered it at total risk of extinction (see also Figure 2F-H where 0.95 of the h_r values in 2070 RCP 85 were below h_r critical assessed in the contemporary). While *G. morafkai* ($P_{persistence} = 0.13$) was at slightly lower risk of extinction it was not considered at risk of total extinction (see Figure 2C-E where 0.87 of the h_r values in 2070 RCP 85 were below h_r critical assessed in the contemporary). Because *G. morafkai* spans both countries and the endangered species act operates in the U.S., we must consider the loss of *G. morafkai* in the U.S. due to climate change, and see that it is not at total risk of extinction in either country, under the 2070 RCP 85 scenario. Both species are projected to benefit in 2070 from an RCP 45 scenario: *G. evgoodei* receives a modest benefit ($P_{persistence} = 0.11$), while *G. morafkai* increases dramatically ($P_{persistence} = 0.49$).

The climate refugia for both species are all disjunct from each other in the 2070 RCP 85 scenario in that they lack migration corridors that might retain gene flow, problematic given the small size of each climate refuge. Under a 2070 RCP 45 scenario for G. *morafkai*, the refugia maintain migration corridors, and given the extensive network of protected areas in southern AZ, the species is a low risk overall. Most of the G. *morafkai* climate refugia have protected areas

already established where the species might persist in the U.S. (e.g. Organ Pipe National Monument, Coronado National Forest, Agua Fria National Monument, Prescott National Forest, Kofa National Wildlife Refuge in the U.S., and other areas that have less impact – Native American Nations) but in Mexico only a two reserve have been established (Sierra el Viejo in Mexico). For G. *evgoodei*, one of the high altitude climate refugia is near an established reserve (Sierra de Alamos-Rio Cuchujaqui Biosphere Reserve) but the reserve will require more extensive surveys given there are no occurrence records in it, as derived from museum records. The other reserve is also at high elevation (Northern Jaguar Reserve) and has a large area favorable as a climate refuge but is outside of the current (known) range of G. *evgoodei*.

For the species G. *sila*, the Blunt-nosed Leopard Lizard, it is listed as an endangered species in the U.S. (an iconic species in that it was the first species listed under the Endangered Species Act) with a recovery plan that requires the establishment of robust populations in 5 parts of the species range (50). This species also has climate refugia at higher elevation sites based on logistic regression of extinction risk and altitude (2070 RCP 45: χ^2 = 749.85, 2070 RCP 85: χ^2 =11.17). Under a 2070 RCP 85 scenario, the species will go extinct from large central portions of the species range at low elevation with only a single large refugium in the Carrizo National Monument, a protected area, and two smaller isolated refugia, one on a high elevation plateau (Panoche Plateau Research Natural Area) above the Panoche Valley and another single site north of the Tejon Conservancy, but not in the Tejon Conservancy that lies to the south. While G. sila is not predicted to go totally extinct under climate change ($P_{persistence}$ = 0.20) under a 2070 RCP 85 scenario, it would benefit under a 2070 RCP 45 scenario ($P_{persistence}$ = 0.29) and the region around the Panoche Valley would become a viable climate refuge with populations on the Panoche Valley floor and uplands of the plateau. There are other threats to the species for Panoche Valley floor populations of G. *sila* (Panoche Valley Preserve), which face potential solar farm development that would negatively impact the core area of their valley floor range.

Our three case studies (Fig. 5, 6) highlight how extinction predictions for 15 reptile families can be further analyzed in the context of high elevation reserves where species might persist under climate change, the first steps in Gap Analysis (*49*). Future studies should combine such analyses in multi-species persistence, involving all 142 species, but such work requires consideration of competition, which might benefit one species under climate change, but threaten another, and also consider the effects of forest per se on climate refugia as noted above.

Range expansions: run up or go north (in elevation or to northern latitudes)

Our assessment of extinction risk may be conservative and restricted to hypotheses related to critical thermal limits being exceeded, but not necessarily other extinction causes such as competition. Besides extinctions in reptiles at low-altitude and low-latitude range limits, extinction at demographic hypothesis of extinction risk and climate change also has a corollary: populations at high elevation near physiological or competitive limits should be undergoing extinctions, while lower elevation species should expand their range to higher latitudes and elevations. Sinervo et al. (*1*) observed 7 cases of range extension in which a species from lower-elevation or lower latitude invaded habitat coincident with local extinction of a high elevation species. These 7 range expansions were from warm to historically cooler climates. The rate of

range expansion is remarkable, when it occurs. For example, *Sceloporus aeneus*, rapidly expanded from below 3000 m to occupy habitat at 3350 m, within a decade based on nearly continuous monitoring of an elevational transect along the Ajusco Volcano (Mexico, DF). Climate change can result in a local improvement for lizards with higher T_b (*51*) that are limited by cold at their high elevation. It is noteworthy that four of seven range expansions were observed when *S. spinosus* invaded, the lizard with the highest T_b of the *Sceloporus* lizards in past surveys. Sinervo et al. (*1*) could explain 18 of 24 extinctions in terms of the null model of eco-physiology, while 8 of the extinctions but seem to be associated with range expansions.

Therefore, in Mexico ~2/3 of observed extinctions were due to thermal causes acting on evolved susceptibility to climate warming, such as low T_b and evolved adaptations such as viviparity (which is also associated with low T_b) that heighten extinction risk from eco-physiological limits being exceeded. However, 1/3 of the extinctions could not be attributable to thermal adaptations, but were explained by a putative competitor that had expanded its range to that site. Thus, predicted level of extinctions due to climate change from both eco-physiology *and* competition may be higher. We adjusted by current levels of extinction (e.g., 2/3 divided into extinctions due to eco-physiology alone, 22% extinction rate) to obtain a less conservative extinction risk assessment. If so extinctions may reach as high as 34% for the desert and tropical montane endemics characteristic of Mexican and Californian Biogeographic Province, when both causes are included. In this regard, we have already observed extinctions of reptiles above the threshold for climate refuges of 2500 m, identified in our risk analysis above, and these extinctions seem to have been associated with invasion of a warm-adapted congener (1). During our fieldwork from 2010-2016 across the study region we have discovered new extinctions of Mexican reptiles, besides those already reported in Phrynosomatid lizards (1), and we are currently testing predictions in this paper against the pattern of extinctions observed across even more diverse reptile families of Mexico, California, Arizona and New Mexico, and in more complex models of the thermal niche that involve equations for competition generated by overlapping thermal niches among congeners.

The simple model of extinction thresholds adopted here can only directly consider the null model of eco-physiology as a cause. Finally, the thermoconforming model of forest conformers adopted for fossorial conformers will require more elaborate information, including the potential for movement among soil horizons of varying depth allowing the species to potentially mitigate warm temperatures by seeking lower temperatures. This analysis will be required to critically evaluate the extinction predictions at the level of family for three reptile families (Anniellidae, Bipedidae, Dibamidae).

Patterns of extinction in 15 families of Mexican reptiles serve as a harbinger for other tropical forest species of lizards with endemic and montane distributions in Central America. Tropical species on other continents (e.g, South America, Asia and Africa) may be undergoing similar local extinctions due to climate change. The concordant extinctions observed in oviparous and viviparous reptiles in Europe, North and South America, African and Australia (1) provides an alarming confirmation that current climate-change extinctions have a global scope and span tropical to temperate habitats, deciduous tropical forests, and jungles to deserts.

Acknowledgements

Figures

Figure 1. The two geographic covariates used in our analysis of extinction risk: A) altitude (rn) and B) level of forest cover, coded 0-4, and C) density plot of occurrence records (black dots).
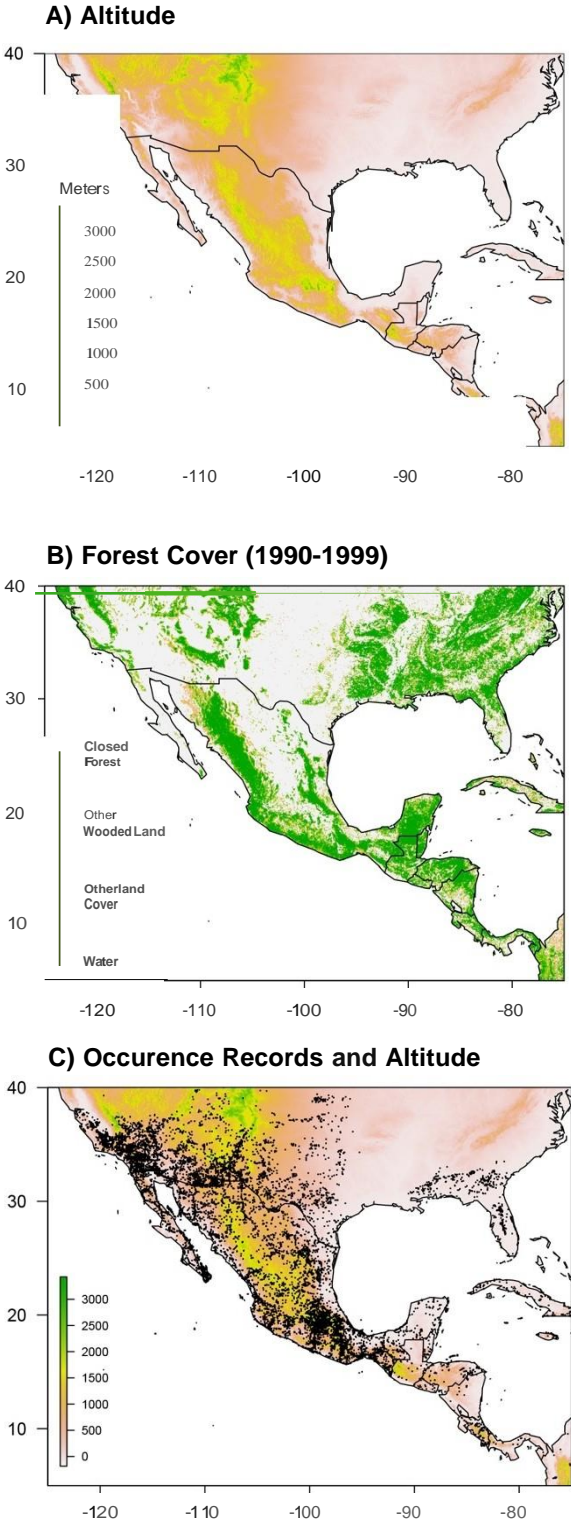
A) Altitude

B) Forest Cover (1990-1999)

C) Occurence Records and Altitude

Figure 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 vs. *Gopherus evgoodei* in tropical deciduous Forest habitats of Sinaloa, respectively. Application of the h_r curve to $T_{max} - T_{pref}$ for the C) Contemporary (1975), under D) 2070 RCP 85 and E) 2070 RCP 45 for *G. morafkai* and F) Contemporary (1975), under G) 2070 RCP 85 and H) 2070 RCP 45 for *G. evgoodei*. In C-H the dashed red line represents the critical h_r (95% upper quantile) used to simulate the upper limit for extinctions in future time points. Values of h_r above the red line are assumed to go extinct.
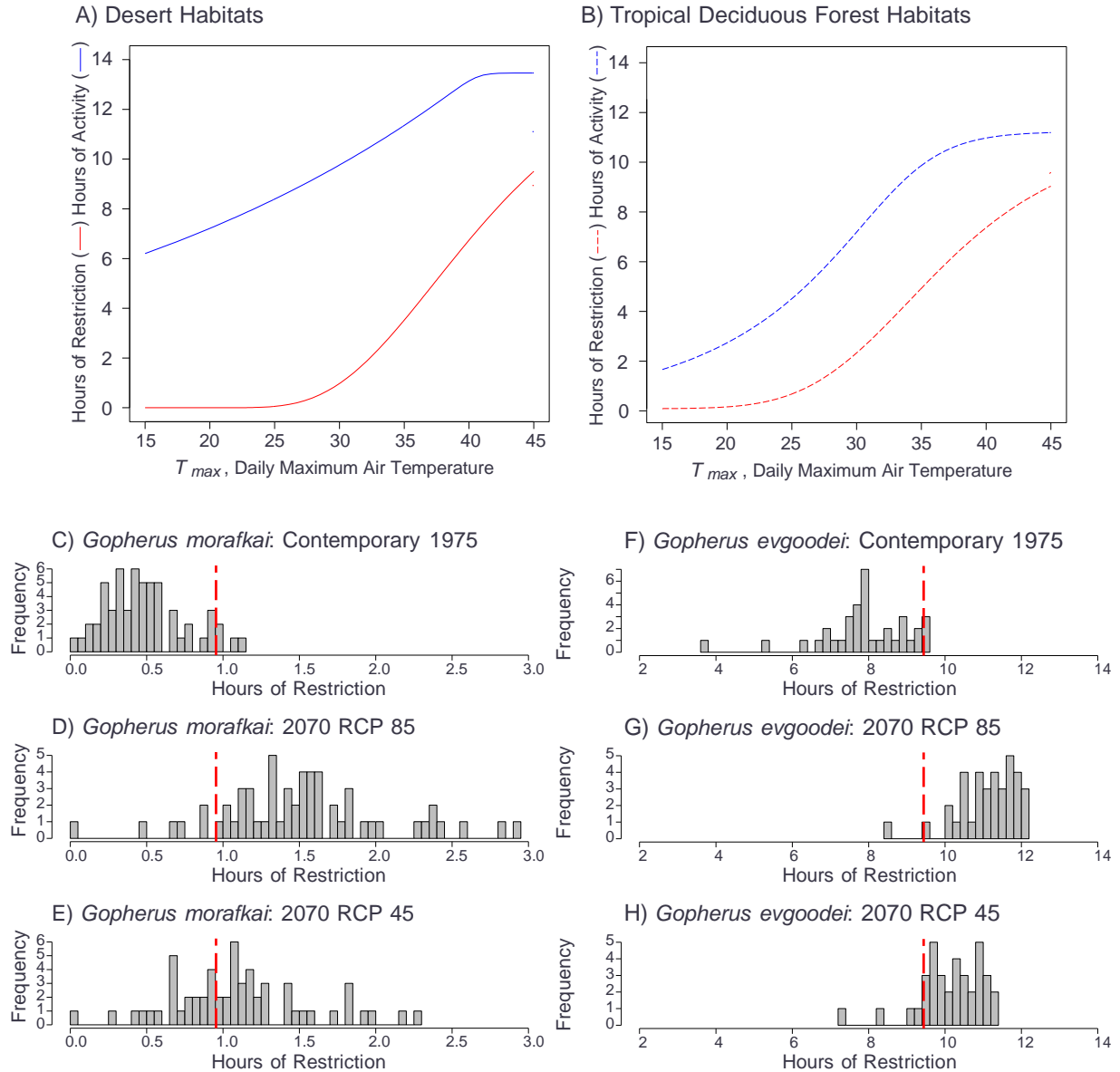
Figure 3. Geographic patterns of persistence vs. extinction risk of reptile families (pooled across 142 species) for 2 time points (2050) and 2 RCP profiles (45 and 85). Probability of population persistence is coded blue (1.0) and extinction is coded red (0.0). Islands of blue in Mexico reflect refuges from climate change at a given time point and are associated with both high altitude and forested regions (c.f., Figure 2AB).

A) 2050 RCP 45

B) 2070 RCP 45
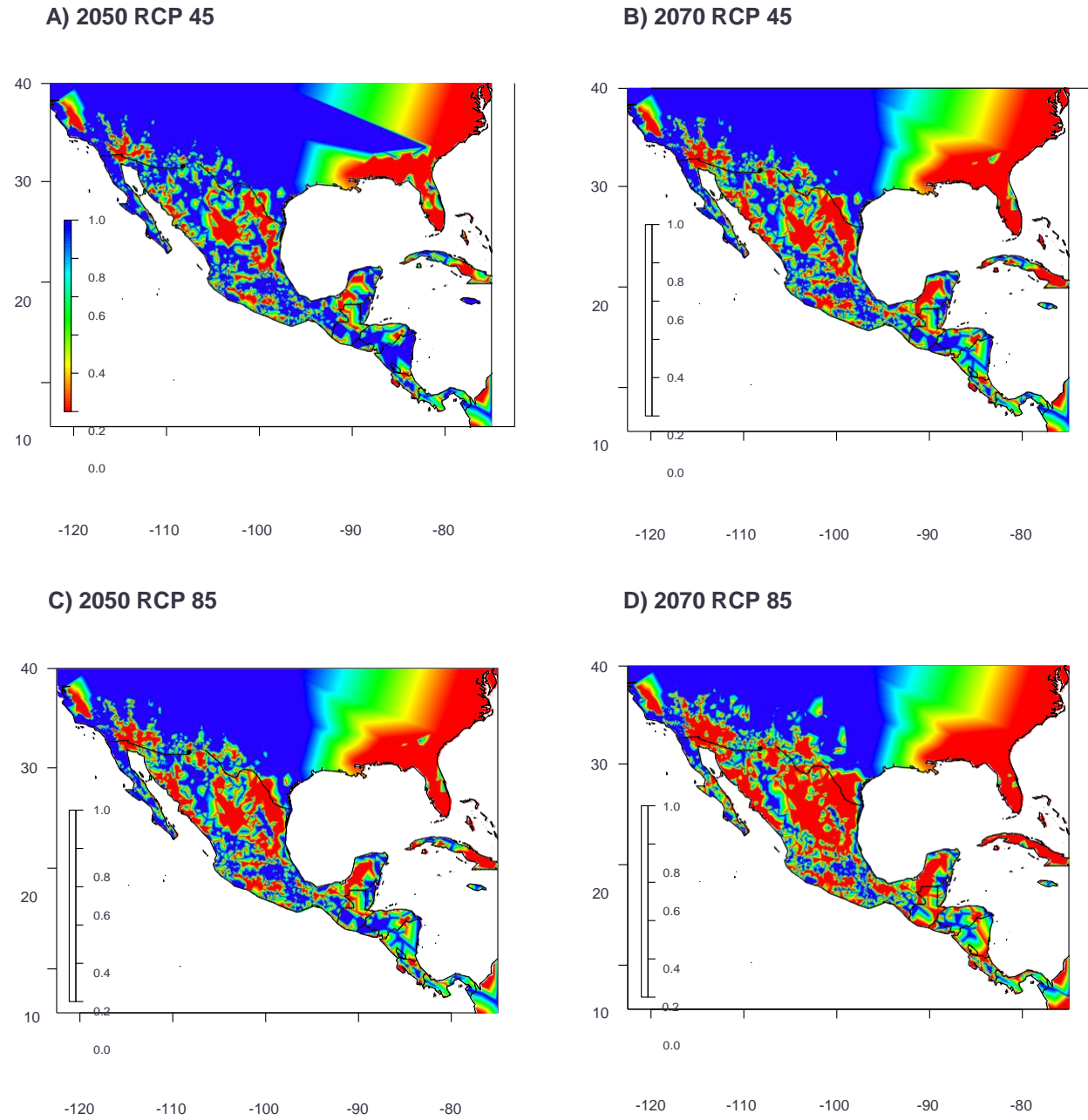
C) 2050 RCP 85

D) 2070 RCP 85

Figure 4. Relative extinction risk (0) or persistence to 2070 as a function of: A) reptile families (coded red for heliotherms vs blue for conformers, Testudinae in black has both heliothermic and conforming species), B) covariates for Forest Cover under RCP 45 and C) RCP 85 and D) Altitude (m) under RCP 45 and E) RCP 85.
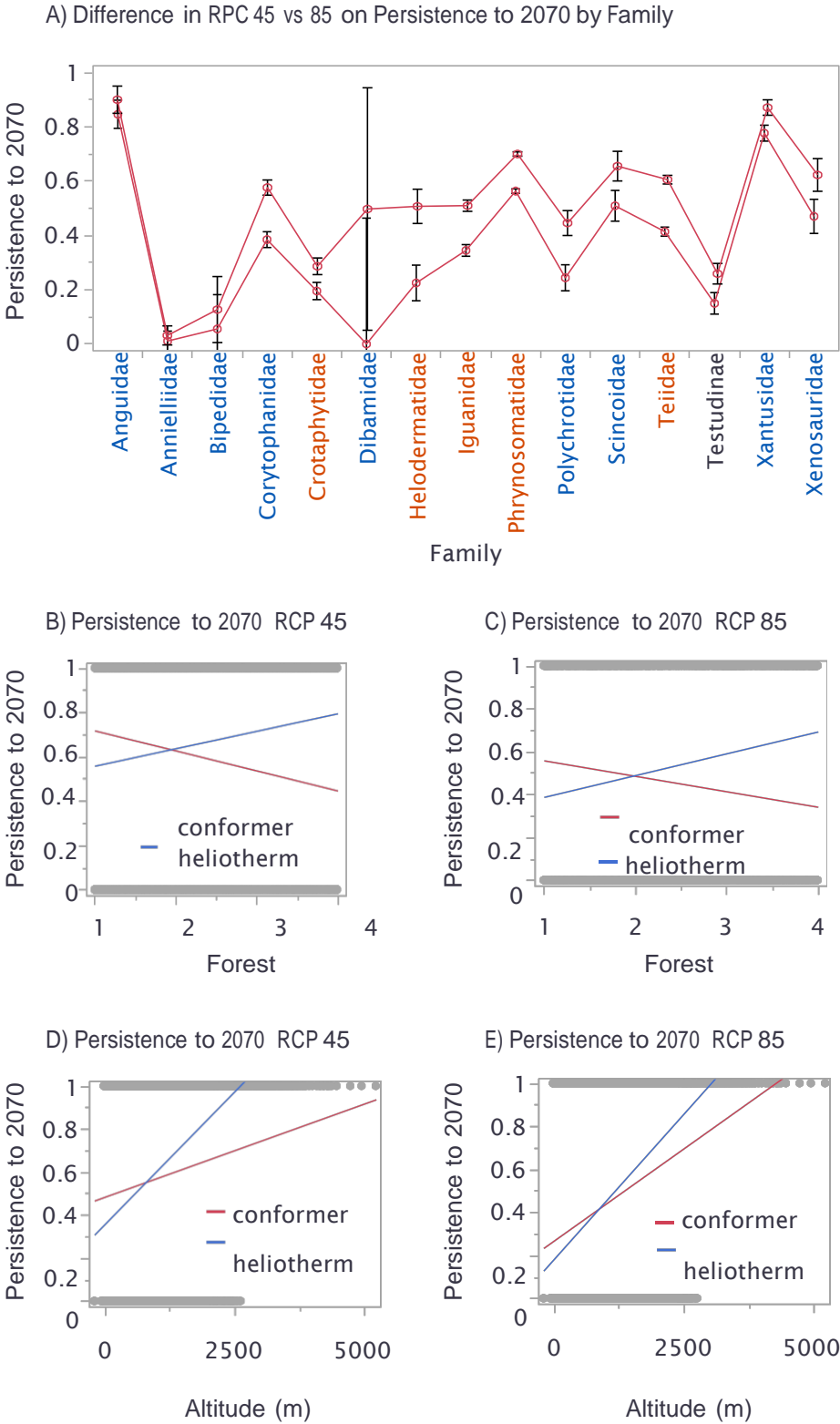

A) Difference in RPC 45 vs 85 on Persistence to 2070 by Family

B) Persistence to 2070 RCP 45

C) Persistence to 2070 RCP 85

D) Persistence to 2070 RCP 45

E) Persistence to 2070 RCP 85

Figure 5. Extinction risk for *Gopherus morafkai* and *G. evgoodei* for 2 time points (2050, 2070) and 2 RCP profiles (45 and 85). Probability of population persistence is coded blue (1.0) and extinction is coded red (0.0). Predicted climate refugia are located in the islands of blue (persistence = 1), which high elevation sites.
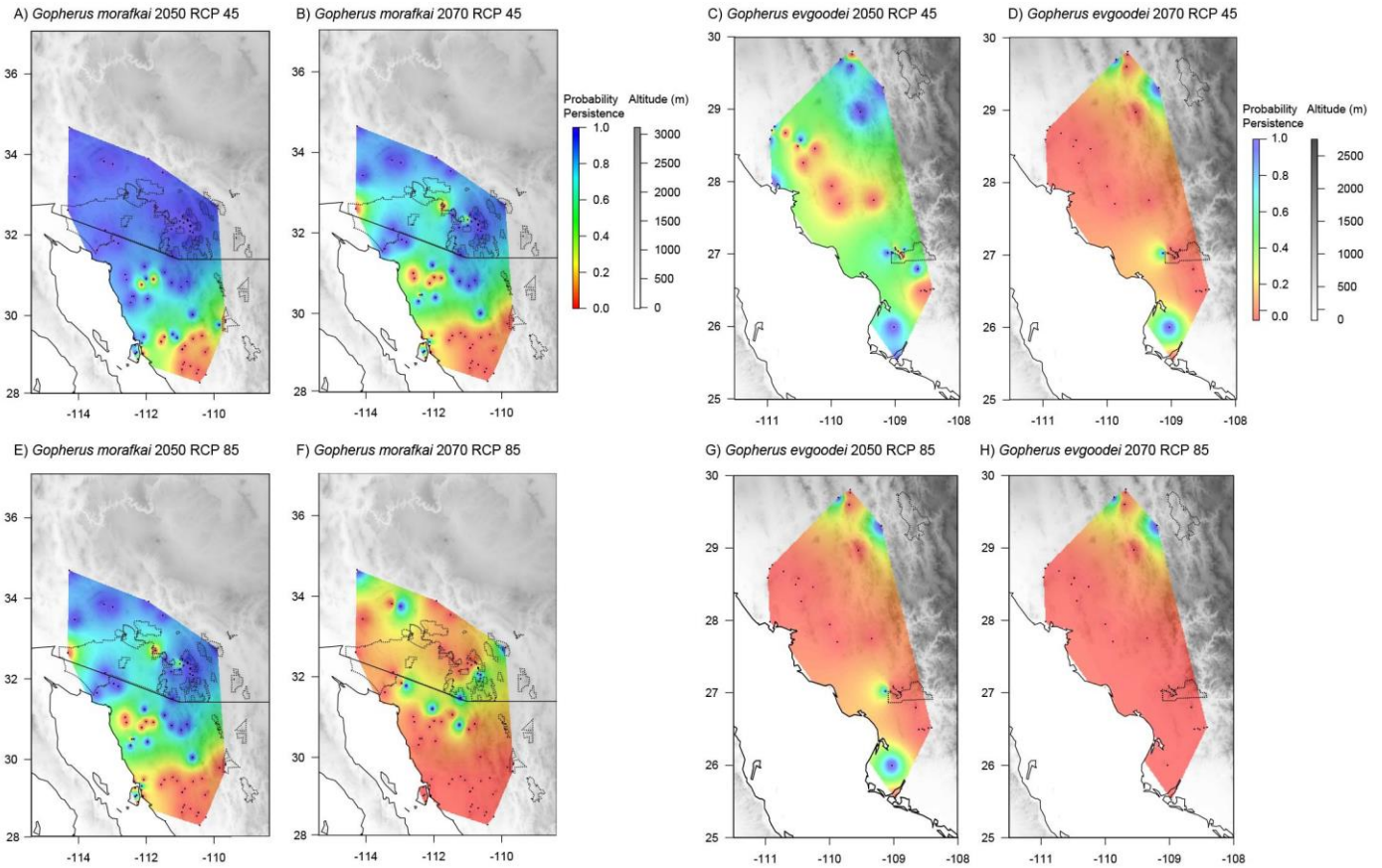
Figure 6. Extinction risk for *Gambelia sila* in the Central Valley of California for 2 time points (2050) and 2 RCP profiles (45 and 85). Probability of population persistence is coded blue (1.0) and extinction is coded red (0.0). Islands of blue to the west are located at high elevation sites. The black polygon labeled CPNM reflects a protected site at one climate refuge, the Carrizo Plain National Monument, while the inset map highlights a currently unprotected site, the Panoche Valley (black polygon labeled PV), which is a climate refuge under RCP 2070 85, but is currently proposed for protection (Panoche Valley Preserve, it will be owned / managed by Center for Natural Lands Management), while the Panoche Plateau Research Natural Area (dashed-white and black polygon labeled PP) is protected and under BLM management.
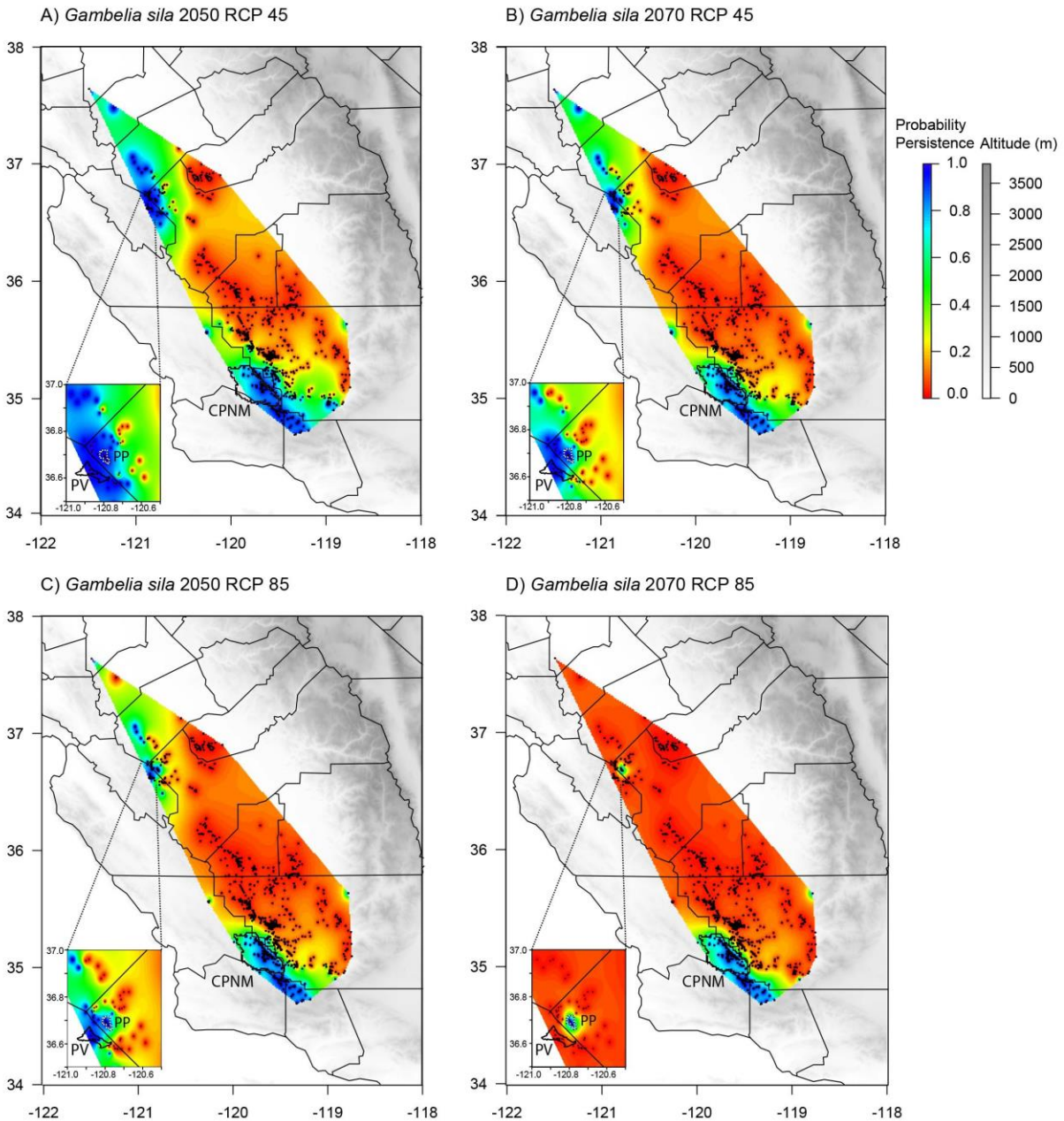
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