Climatic niche contraction, habitat restoration opportunities, and conservation biogeography in California's San Joaquin Desert

Running title: Conservation biogeography of the San Joaquin Desert

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PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.26758v1 | CC0 Open Access | rec: 23 Mar 2018, publ: 23 Mar 2018

Conceived the study: JAES, BS, HSB, MFW; Contributed data: JAES, JQR, ENT, BS, MFW; Analyzed data: JAES; Led the writing: JAES; Contributed to the writing of the paper: JQR, HSB, DJG, BS, MFW.

Acknowledgements

We thank T. Bean and R. Kelsey for incisive comments on early manuscript drafts. Occurrence data was contributed by R. Hansen, A. Kuritsubo, D. Hacker, R. McCormick, and K. Sharum. J. McLeod assisted with review of aerial imagery at historical occurrence locations. Funding was provided by BLM, TNC, CDFW, NSF (EF-1241848), and ISEECI.

Abstract

Aim: Habitat loss has been the greatest historical driver of species extinctions. A recent global trend toward retirement of marginally productive agricultural lands presents opportunities to reclaim critical habitat for endangered species. We examine habitat restoration opportunities in the context of historical sources of habitat loss, including agriculture, development, habitat fragmentation, and invasive-species-mediated climatic niche contraction.
Location: California’s San Joaquin Desert (SJD) is one of the world’s most agriculturally productive landscapes. Fragments of remnant habitat serve as habitat for 34 threatened and endangered species. Retirement of agricultural land in the SJD is being driven by climate change, groundwater salinization, and historical groundwater overdraft—even as unmitigated loss of virgin habitat continues.
Methods: To promote efficient habitat protection and restoration, we conducted a quantitative assessment of habitat suitability, habitat loss, climatic niche stability, projected effects of climate change, and reintroduction opportunities for an umbrella species, the endangered blunt-nosed leopard lizard (*Gambelia sila*).
Results: Analyses indicate that *G. sila* habitat overlaps with occurrence records for 128 vulnerable species and that its habitat is broadly representative of the habitat of other vulnerable species in the SJD. We document an apparent climatic niche contraction for *G. sila* and associated range contraction away from more mesic margins of the historical distribution, apparently driven by introduction of exotic grasses and forbs. We use habitat suitability models, in conjunction with modern and historical land use maps, to estimate historical and modern rate of habitat loss to development and fragmentation. We use NASA fallowed area maps to identify 610 km^2 of fallowed or retired agricultural land with high potential to be restored as habitat. We discuss conservation strategies in light of anticipated climate change and potential for habitat restoration.
Main Conclusions: In the midst of multiple sources of historical and ongoing habitat loss, farmland retirement presents an opportunity to recover large amounts of endangered species habitat.

Keywords: endangered species, extirpation, farmland retirement, invasive species, range contraction, reintroduction

1. Introduction

Global habitat loss, resulting mainly from agricultural expansion, has been the greatest historical driver of extinction (Baillie et al., 2004; Foley et al., 2005). A recent global trend toward retirement of marginal farmland, especially in temperate latitudes, presents an important opportunity to reclaim some of this lost habitat in a cost effective manner (Queiroz et al., 2014). While future land-use trends are uncertain (Alexandratos & Bruinsma, 2012; Ausubel et al., 2012), recent trends toward farmland retirement presents an important opportunity to reclaim habitat of vulnerable species before land is claimed for other uses (e.g., Pearce et al., 2015). To better understand this opportunity, we investigate land use and potential habitat restoration in one of the world's most agriculturally productive landscapes, California's San Joaquin Desert (SJD).

Despite the presence of 34 threatened and endangered species, agricultural expansion continues to drive habitat loss in the SJD, even as marginal lands are retired (Williams et al., 1998; Table S1). Conversion has been driven primarily by agricultural expansion and spread of exotic grasses and forbs (Germano et al., 2011). Agricultural expansion has been enabled by water exports from northern California and groundwater overdraft, leading to conversion of even agriculturally marginal land (Shumway, 1973). For instance, most farmland in the western SJD now suffers from salinization due to irrigation of saline soils with low permeability clay layers (Cismowski et al., 2006), making irrigated agriculture unsustainable (Schoups et al., 2005). Climate change in the SJD has also contributed to reduced water availability and increased evaporation (AghaKouchak et al., 2014; Griffin & Anchukaitis, 2014; Wang & Hipps, 2014). As a result of salinization, historical overdraft, and climate change, a trend toward multi-year fallowing has emerged in recent decades, particularly during California's unprecedented mega-drought, from 2012 to 2015. In 2015, over 4,100 km^2 of irrigated SJD farmland were fallowed (Melton et al., 2015). The trend toward permanent retirement of farmland is projected to continue as climate change exacerbates drought stress and basins come into compliance with California's Sustainable Groundwater Management Act (Hanak et al., 2017). With proper retirement and restoration in strategically selected areas, these lands could again serve as critical habitat for endangered species.

Reclaiming this lost habitat could contribute to recovery of dozens of threatened and endangered species. However, it is unclear which lands in the SJD represent the most efficient investment for species recovery. In this study, we developed habitat suitability models for an umbrella species of the SJD, the endangered blunt-nosed leopard lizard (*Gambelia sila*). We focus on *G. sila* because our analyses indicate that its habitat is most representative of habitat of other upland endangered species of the SJD (see sections 2.2, 3.1). We apply our ensemble habitat suitability model to estimate the historical distribution, quantify habitat loss over time, assess conservation value of currently intact natural habitats, identify retired agricultural parcels with high potential to again serve as habitat, and forecast effects of climate change. Our models are mechanistic in that they incorporate variables that govern physiological temperature limits of reptiles under climate warming (Sinervo et al., 2010) and hydroclimatic constraints on ecosystem productivity and composition (Webb et al., 1978; Hawkins et al., 2003). The models are also correlative in that they derive parameter values from statistical relationships with occurrence records. Unlike previous models of SJD habitat suitability (Bean et al., 2014; Pearce et al., 2015; but see Cypher et al., 2013; Table S2), our models are appropriate for assessing habitat restoration potential on retired farmland because they properly account for anthropogenic land use.

2. Methods

2.1 *Study system*

California's San Joaquin Valley is one of the most agriculturally productive regions of the world and across 8 counties it generated $25.9 billion in 2010 (CDFA, 2013). We focus analyses on the associated ecoregion, the San Joaquin Desert (SJD), which historically encompassed 28,493 km^2 including western and southern two-thirds of the San Joaquin Valley, as well as the Carrizo Plain and Cuyama Valley, to the southwest. The SJD experiences a Mediterranean climate regime with average yearly rainfall from 280 mm in the northwest to 117 mm in the south (Germano et al., 2011). The SJD once supported extensive upland habitat composed of alkali sink scrub, saltbush shrub (*Atriplex* spp.), *Ephedra* scrubland, and grassland dominated communities as well as a vast aquatic system of lakes, rivers, marshes, and sloughs fed by rainfall and snowmelt from the Sierra Nevada. Today, most native habitat has been converted to row crops and orchards, remnant upland habitat is heavily impacted by exotic annual grasses and forbs, and wetlands have been drained to support agriculture (Wester, 1981; Nelson et al., 2003; Kelly et al., 2005). As a result, 34 species found within the SJD are currently listed as threatened or endangered (Table S1).

2.2 *Umbrella species evaluation*

We sought to evaluate the "umbrella species performance" of *G. sila* and habitat overlap of other threatened and endangered upland species of the SJD. We started with nine upland threatened and endangered species, all with a majority of their California Natural Diversity Database (CNDDB) occurrence records falling within the SJD and with at least 10 occurrence record locations on intact habitat (Table S1). We used MaxEnt and nine environmental predictor variables (Table S3) to build habitat suitability models for the nine candidate umbrella species based on CNDDB occurrence locations for target species. Background records used for model parameterization included all VertNet (VetNet.org) record locations for vertebrate species. Occurrence and background records were thinned to one record per 1-km grid cell and historical records on habitat currently extirpated to development were excluded. We did not use hinge and threshold features to reduce overfitting and model complexity. Habitat suitability models for each species were evaluated, using their area under the receiver operating characteristic curve (AUC) scores, for their ability to distinguish occurrence and background locations for each of the nine candidate umbrella species (Bonn et al., 2001). We used a uniform set of background locations to determine AUC scores for all species, composed of all unique VertNet occurrence locations (reduced to one record per 1-km grid cell) spanning the collective distribution of thresholded habitat suitability (i.e., true positive rate equal to true negative rate) for the full suite of nine candidate species.

Following the identification of blunt-nosed leopard lizards (*Gambelia sila*) as the top-performing umbrella species (Section 3.1), we focused subsequent analyses on habitat for this species. Their distribution is entirely limited to the SJD where their habitat requirements are generally representative of other upland threatened and endangered species (Bradford, 1992; Germano et al., 2011). They were among the first species protected under United States law in 1967 (Udall, 1967) and remain listed as endangered today. Their status is mainly a result of habitat loss and fragmentation due to agricultural land conversion, urbanization, energy development, and invasion of non-native vegetation (USFWS, 2010). *Gambelia sila* inhabit relatively flat, sparsely vegetated areas of the SJD including the valley floor, surrounding foothills, and valleys to the southwest (Germano & Williams, 1992; Williams et al., 1998; Germano et al., 2011).

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2.3 *Occurrence data*

We used 618 geographically unique *G. sila* occurrence records to develop habitat suitability models. We obtained occurrence data from publicly available data portals (e.g., VertNet.org, GBIF.org), the CNDDB, correspondence with professional biologists, the literature, and from surveys conducted by the authors of this paper. We corrected for sample bias (Schulman et al., 2007; Kramer-Schadt et al., 2013; Syfert et al., 2013) by using all geographically unique vertebrate occurrence records, within 50 km of occurrence locations, as background or pseudo-absence data (n = 6,285). We did not consider background data within the distribution of *Gambelia wislizenii* because of evidence of introgression (Grimes et al., 2014; Richmond et al., 2017), potential for competitive exclusion between these congeners (Means, 1975), and topographic barriers to dispersal. We thinned occurrence and background data to one record per 1-km grid cell to reduce geographic aggregation and spatial sorting bias. We removed areas from model training where occurrence intensity was biased by current land use (e.g., agricultural and urban areas; section 2.6), allowing our model output to be used as a metric of habitat quality not just on intact habitat, but also as a metric of pre-development habitat quality on lands that have been lost to development.

2.4 *Environmental data*

We developed habitat suitability models using 11 candidate predictor variables known or hypothesized to be important to *G. sila* natural history, demography, and distribution (Table S3; Montanucci, 1965; Westphal et al., 2016). The 11 variables were composed of continuous metrics of climate (mean annual precipitation [MAP], climatic water deficit [CWD]), thermal physiology (hours of restriction [H_r], hours of activity [H_a]), vegetation productivity (normalized difference vegetation index [NDVI], actual evapotranspiration [AET]), soil properties (percentage clay, pH, electrical conductivity), and habitat suitability for a keystone taxon in *G. sila* habitat, kangaroo rats (*Dipodomys*), whose precincts and burrows generate high quality refugia (Goldingay et al., 1997; Prugh & Brashares, 2012). We obtained or derived climate, thermal physiological, and evapotranspiration data from the basin characterization model (270 m resolution, mean values for 1981–2010; Flint and Flint 2012). We estimated hours of restriction and hours of activity, the number of hours per day that temperatures are too hot or hot enough for *G. sila* activity, by regressing operative environmental temperature (Dzialowski, 2005) data from 12 sites spanning the distribution of *G. sila* against maximum daily air temperature data at those sites (Fig. S1; Sinervo et al., 2010). We deployed 4 models per site in both sun and shade habitats, and thus, 24 models across the species range of two sizes, medium-large (22 × 4 cm) and large PVC (25 × 6 cm), all painted grey, suitable for computing hours of restriction in *G. sila*. We derived soil data for surface horizons from Soil Survey Geographic Database (SSURGO) polygons and filled missing areas with values estimated from satellite data (Hengl et al., 2014, 2015; Gozdowski et al., 2015). We derived average NDVI data from MODIS satellites measurements at 16-d temporal resolution and 250-m spatial resolution, over the period 2001–2010. We derived slope from 30-m resolution national elevation dataset (NED) raster grids. We estimated *Dipodomys* habitat suitability as a function of nine predictor variables (Table S3), using a MaxEnt model parameterized with *Dipodomys* occurrence locations spanning California.

2.5 *Model selection and evaluation*

We evaluated 236 models, which included all possible, uncorrelated ($|r| < 0.8$) combinations of up to five of the 11 candidate predictor variables (Burnham & Anderson, 2002). We parameterized models with MaxEnt version 3.3.3k. We turned off hinge and threshold features to reduce overfitting and model complexity and to produce more mechanistically interpretable response curves. Performance metrics we used to evaluate models included change in Akaike's information criterion (ΔAICc), AUC, Boyce Index (BI), and unregularized training gain (Gain). We combined models with > 1% AICc model weight by implementing multi-model averaging. We then used our resulting ensemble habitat suitability model to estimate historical distribution and habitat quality on intact and converted lands, and to project potential climate-mediated changes in habitat suitability. We thresholded continuous suitability values into suitable and non-suitable areas using the threshold that maximized the true positive rate and true negative rate. We used MIROC-ESM RCP8.5 drought scenario to project potential changes in habitat suitability for 2050 and 2080. We chose this scenario because RCP8.5 most closely represents our current greenhouse gas emission trajectory (Peters et al., 2013) and because climate change is predicted to worsen drought conditions in the SJD (Pierce et al., 2013; Diffenbaugh et al., 2015). We also assessed current limiting environmental factors for *G. sila* across geographic space. We identified the limiting covariate for each grid cell as the covariate providing the greatest increase in habitat suitability if the covariate value was adjusted to its mean value across occurrence locations.

2.6 *Habitat loss and extirpation*

We estimated amount of habitat loss from agricultural, urban, and industrial development by overlaying our map of predicted historical distribution onto contemporary and historical land use maps. We obtained historical land use maps for the years 1945, 1960, and 1990 from the Central Valley Historical Mapping Project (Nelson et al., 2003; Olmstead & Rhode, 2003). Land use categories for 1990 were further refined using historical farmland maps from the California Farmland Mapping and Monitoring Program. We obtained contemporary (2015) land use maps from the California Fire Resource and Assessment Program and modified them by hand in accordance with aerial imagery. We used a statistical relationship between habitat patch size and probability of *G. sila* occupancy (Bailey & Germano, 2015) to estimate per-site probability of occupancy and total amount of habitat loss caused by fragmentation.

We assessed habitat loss at *G. sila* historical locations (i.e., extirpation) by reviewing records in the vicinity of areas of development to determine if spatial information (e.g., aerial imagery, land use maps) associated with the records were sufficient to conclude that the habitat had been lost. From 1989–2016, during spring breeding (March to June), we extensively resurveyed two historical record locations on undeveloped habitat at or near the northern limit of the species historical distribution to determine if the species persisted at those sites (Table S4). We used parametric and nonparametric tests to assess our *a priori* hypothesis that dense herbaceous vegetation was responsible for these extirpations (Germano et al. 2001, 2012). We tallied areas of potential extirpation on intact habitat, where the species was documented historically but has not been seen for decades. We reduced historical (pre-1995) records from intact habitat to one unique occurrence location per 5-km resolution grid cell. We flagged unique historical localities that lacked corresponding recent (1995–present) records within a 5-km radius as areas of potential extirpation. This study complies with the University of California, Santa Cruz policy regulating research on animals through a permit to conduct a UCSC Live Vertebrate Animal Study—Non-Bio- medical, granted by the UCSC Institutional Animal Use and Care Committee, permit #Sineb1402.

2.7 *Habitat protection and potential for restoration*

We used annual fallowed area maps produced by NASA (Melton et al., 2015) in conjunction with our *G. sila* historical habitat suitability maps to map the extent of formerly-suitable *G. sila* habitat that was converted to agriculture but that has since been continuously out of agricultural production for the period 2013–2015. We considered these areas to be either retired or have high potential for permanent retirement from agricultural production. We used clumping analysis to identify the areas of retired land that, if restored, and in conjunction with existing intact suitable habitat, would constitute continuous areas of suitable habitat ≥ 4.94 km^2 in size. The 4.94 km^2 cutoff represented the minimum patch area sufficient for a > 90% probability of local population persistence over the historical era (Bailey & Germano, 2015). We used the California Protected Areas Database, the California Conservation Easement Database, and knowledge of additional areas under conservation easement, to identify areas of intact habitat that are currently either protected or not protected from habitat loss. *Gambelia sila* is a fully protected species, and no loss of habitat is permitted under state law. However, these protections are largely unenforced on private lands (see section 3.4). We used clumping analysis to identify potentially vulnerable areas of unprotected habitat that currently contribute to large areas of intact habitat ≥ 4.94 km^2 in size.

3. Results

3.1 *Umbrella species evaluation*

Among the nine candidate umbrella species, the habitat suitability model for *G. sila* performed best in predicting the distribution of all other candidates (Fig. S2). The mean AUC score for the *G. sila* habitat model, the average of the model's AUC scores for each of the candidate species, was 0.703 (range = [0.574, 0.880]). The habitat suitability model for one other species, *Dipodomys nitratoides nitratoides*, performed nearly as well, with a mean AUC score of 0.690 (range = [0.586, 0.934]). The mean true positive rate for the thresholded *G. sila* model was 0.752, indicating that areas predicted to be suitable encompassed, on average, 75.2% of the occurrence locations for the other candidate species. These results suggest that *G. sila* may be the most effective single umbrella species for upland species of the SJD.

3.2 *Predicted habitat quality and distribution*

The best performing model of current habitat suitability for *G. sila* (ΔAICc = 3.52, AUC = 0.93) identified, in decreasing order of variable contribution, NDVI, H_r, slope, percentage clay, and electrical conductivity as the most important drivers habitat suitability (Table 1A). This model had high utility as a predictor of current habitat suitability, but was not appropriate for forecasting or hindcasting because of the limited temporal span of the satellite derived vegetation index, NDVI. To achieve temporal transferability, we performed a second iteration of model selection, limited to the 197 candidate models that did not include NDVI as a predictor variable. In lieu of NDVI, the resulting best-performing models identified hydroclimatic correlates of vegetation productivity (AET, MAP) as the most important predictor variables.

The best performing temporally-transferable habitat suitability model, which consisted of the weighted average of the top two performing models, incorporated six environmental variables: MAP, AET, slope, percentage clay, electrical conductivity, and pH (Table 1B). This ensemble model incorporated 100% of inter-model Akaike weight and also achieved a high AUC score of 0.93. We use this model for all subsequent analyses and figures. Two variables (MAP, AET) indexed hydrology and were related to preference for low herbaceous vegetation density. One variable (slope) is a measure of topography: *G. sila* seems to prefer relatively flat habitat. Three variables measured soil characteristics: *G. sila* appears to have an affinity for lower clay content, more alkaline and moderately saline soils, perhaps because these characteristics increase friability and reduce vegetation productivity (Fig. S3).

The model threshold that maximized the true positive rate and true negative rate, 0.206, successfully classified 94% of distinct occupancy locations as suitable habitat and classified 81% of background locations (where other species were detected) as unsuitable. These rates suggest that about 6% of real suitable habitat is unaccounted for, and that some areas outside of our mapped suitable-distribution are perhaps occupied. If detection effort is biased against areas where the model fails to predict suitable habitat, then more than 6% of suitable habitat could be missed by the model. Conversely, the thresholded model likely misclassified some of the non-suitable areas as suitable, though without true absence data or repeat visit data, it is not possible to accurately estimate the amount.

The modeled distribution (Fig. 1) includes central gaps, which correspond to the historical Tulare, Kern, and Buena Vista Lakes, where soil conditions remain unsuitable. Areas of highest predicted habitat quality were found in Kern County, southwestern Tulare County, and on alkaline soils of western Fresno County, including large portions of Westlands Water District (Fig. 2; Fig. S4). The predicted suitable habitat of *G. sila* encompassed occurrence locations for 128 other endangered, threatened, or vulnerable species of the SJD (as classified by the CNDDB; includes upland and wetland species) and contained the majority (≥ 50%) of unique occurrence locations for 40 of these species.

3.3 *Habitat protection and potential for restoration*

We identify 1,007 km^2 of potentially retired farmland (continuously fallow 2013–2015) located on formerly suitable habitat for *G. sila*, and potentially suitable for habitat restoration and reintroduction. Narrowing our search to prioritize large patches of habitat (> 4.94 km^2), with high probability (> 90%) of *G. sila* population persistence based on patch size, we identify 610 km^2 of retired farmland that, with restoration, and in conjunction with existing habitat, would form these large patches of habitat (Fig. 1). We identify 5,371 km^2 of intact and suitable *G. sila* habitat that are not currently protected under public ownership or conservation easement. Ninety-one percent (4,903 km^2) of this intact unprotected habitat contributes to large patches of habitat (> 4.94 km^2).

3.4 *Habitat loss and extirpation*

We estimate that 13,568 km^2 of *G. sila* habitat has been directly lost to agricultural and urban development, comprising 66% of the predicted suitable range of the species. An additional 2.1% (437 km^2 / 20,610 km^2) of habitat has been lost to fragmentation caused by development. Of the remaining habitat, 26% (1,799 km^2 / 7,041 km^2) is protected as public land or under conservation easements, comprising 8.7% (1,799 km^2 / 20,610 km^2) of the original suitable habitat for the species. The rate of habitat loss from agriculture and development appears to have peaked during the 1940s and 1950s, during which time 4,544 km^2 of habitat was lost (Fig. 3). Since 1960, an additional 2,971 km^2 of habitat was lost to agricultural and urban development. Since protection under the US Endangered Species Preservation Act in 1967 (i.e., forerunner of the 1973 US Endangered Species Act [ESA]), we estimate that 2,021 km^2 of *G. sila* habitat was lost to agricultural and urban development. One hundred and five historical occurrence locations for *G. sila* have been converted to agriculture or other forms of development and were classified as extirpated. At least 45 occurrence locations where the species was documented after federal protection in 1967 have since been lost to agriculture, urbanization, damning of reservoirs, and other forms of development. Thirty-five of those losses occurred after the species became fully protected under California law in 1970. Many of these lost habitat patches served as corridors connecting larger patches of natural habitat with documented presence of endangered species. At least eight documented occurrence locations were converted to agriculture during the last decade (2007–2016; Table S5).

We also document extirpations on undeveloped, apparently intact, habitat. We did not detect *G. sila* after extensive resurvey effort at two historical occurrence locations on apparently intact habitat at, or near, the former northern range limit of the species (Fig. 1; Table S4). These extirpated sites had significantly higher AET (i.e., vegetation biomass) than 14 extant localities we surveyed for *G. sila* in 2014 (Wilcoxon's signed rank test, $P < 0.05$), and significantly higher AET than 307 recent record locations where the lizard has been recorded since 1995 (Wilcoxon's signed rank test, $P < 0.01$; Fig. 4). The vegetation at northern extirpated sites was dominated by dense exotic grasses and forbs.

AET was significantly higher across all distinct historical (pre-1960) occurrence locations on intact habitat than at modern (1995 and after) distinct occurrence locations (Wilcoxon's signed rank test, $P < 0.001$; *t*-test, $P < 0.001$; Fig. S5). A total of 103 geographically distinct pre-modern (pre-1995) record locations on intact habitat lacked modern (1995–present) documentation of local persistence within 5 km of a historical location; we flagged these sites as potentially extirpated. Potentially extirpated sites comprise 49% (103/211) of distinct pre-modern occurrence locations on intact habitat. The most recent observation at 50 of these potentially extirpated historical sites was from before 1980. The most recent observation at 16 of these sites was before 1960. AET was higher at sites where the lizards had not been seen for longer for each of four time-since-last-detection categories (Kruskal-Wallis rank sum test, $P < 10^{-14}$; Fig. 4).

3.5 *Impact of climate change*

Projected drought conditions suggest that future climate change could partially mitigate the apparent vegetation-mediated climatic niche contraction documented in this study. Drought conditions are projected to result in reduced vegetation productivity (AET) and general northward expansion of suitable habitat area (Fig. 2). By 2050, climate change is projected to result in renewed habitat suitability at two historical occurrence locations, at or near the species former northern range limit, where we documented apparent vegetation-mediated extirpation and climatic niche contraction. These same climate change projections indicate that suitable habitat could also expand southward and upslope to form a corridor of suitable habitat connecting the range of the blunt-nosed leopard lizard, *G. sila*, with the range of the long-nosed leopard lizard, *G. wislizenii*.

4. Discussion

4.1 *Potential for restoration and reintroduction*

Habitat suitability models can guide reintroduction efforts into formerly occupied portions of the species' range, particularly when used in combination with genetic information (Chauvenet et al., 2013). We identify 610 km^2 of potentially retired (fallow 2013–2015) agricultural land that, prior to development, was suitable habitat for *G. sila* and other endangered species. Prime areas for restoration and reintroduction include portions of Westlands Water District, where at least 405 km^2 of agricultural land is being retired due to the effects of salinization and poor drainage. Our model indicates that western portions of this area may be suitable for restoration and reintroduction (Fig. 2, Fig. S4). Other areas with high potential for restoration include patches of habitat that could form corridors connecting larger patches. One such area is located near Madera Ranch. Recolonization by *G. sila*, and other endangered species, onto retired agricultural land has unfolded over many years in the Carrizo Plain and Panoche Valley (Table S6). Concomitant restoration of native vegetation, including shrubs, and keystone species such as kangaroo rats (*Dipodomys* spp.) could accelerate the process of reestablishing vulnerable species and may be necessary (Germano & Rathbun, 2016).

Genetic data should augment habitat suitability models in identifying appropriate source populations for repatriation on to restored lands, and such data have recently become available (Richmond et al. 2017). One strategy is to select translocation candidates from lineages that are consistent with the species' phylogeographic history for a given region, as these individuals are likely to possess appropriate genetic variation for maintaining demographic and evolutionary stability. Because climate change is also a concern, preserving genetic variation that potentially maintains or enhances fitness under future climate scenarios should also be considered (Harris et al., 2006). With increasing drought severity, for example, it may also be prudent to translocate, *G. sila* from more drought prone (i.e., potentially drought adapted) southern San Joaquin Valley populations to northern sites with less extreme drought conditions. This climate-matching approach would involve a balancing act between infusing beneficial genetic variation from a small number of donors (i.e., immigrants) while at the same time taking precautions to avoid the dilution of locally adapted variation (Mills & Allendorf, 1996; Tallmon et al., 2004; Funk et al., 2012). Even small amounts of immigration should be sufficient to increase genetic variation for selection to act upon, in addition to lowering the frequency of deleterious alleles.

The prospect of restoring land that no longer has agricultural value may represent a cost-effective means of habitat conservation; however, more knowledge and experimentation is needed to understand the timeline and parameters that influence habitat suitability for threatened and endangered species on such lands (but see Laymon et al., 2010). If success can be demonstrated, restoration could serve in tandem with protection of undisturbed lands as an effective strategy for recovery of threatened and endangered species, both in the SJD and on a global scale.

4.2 *Conservation Trajectory*

Endangered species protection has slowed rate of habitat loss in the SJD, but has not halted or reversed the process (Fig. 3). The estimated amount of *G. sila* habitat lost since the species became protected is greater than the total amount of habitat currently protected through public ownership and conservation easement. Unmitigated habitat loss to agricultural and other land conversion continues on large parcels of habitat, including areas with documented *G. sila* occurrence, areas adjacent to protected lands, and areas that formerly served as corridors connecting large patches of habitat (Table S5). These trends appear to be generalizable to other upland endangered species of the SJD.

Conservation of habitat has not, in itself, always guaranteed endangered species population persistence. Even in areas under active management (e.g., vegetation restoration, grazing to thin excess herbaceous growth, etc.), such as Allensworth Ecological Reserve, Pleasant Valley Ecological Reserve, and Pixley National Wildlife Refuge, *G. sila* populations have declined precipitously since the 1990s (USFWS, 2010). Conversion from native shrub and bunchgrass-dominated communities to exotic-dominated annual grassland appears to be responsible for northern range contraction, where habitat remains undeveloped. Before European colonization of California, native habitat for the lizards provided areas of relatively bare soil (Wester, 1981), important for lizard locomotion while hunting and evading predators, and for basking. Today, widespread invasion by exotic annual grasses and forbs has resulted in dense thatch that precludes these behaviors, and reduces survival (Montanucci, 1965), particularly in northern and western parts of the species range where higher precipitation adds to herbaceous productivity. Many invasive plant species that affect *G. sila* were first introduced to California more than a century ago, however the full effects of biological invasions can take millennia to unfold (Crooks, 2005; Strayer et al., 2006). Though the interaction of exotic grasses and climate during the 20th century appears to have resulted in extirpation of these more-mesic sites, 21st-century drought conditions in California are projected to improve habitat suitability for these sites, including extirpated sites we resurveyed, suggesting that reintroduction may be an important conservation strategy for *G. sila* under anticipated climate regimes (Fig. 2; Westphal et al., 2016; supplementary online text).

The high proportion (49%, 103/211) of historical (pre-1995) occurrence locations on intact habitat where *G. sila* have not been documented for over two decades is of great concern. *Gambelia sila* have not been recorded at 24% (50/211) of these locations since 1980, and 8% (16/211) have no record since 1960. Results of this study suggest that many of these sites have experienced vegetation conversion from native communities to exotic, annual dominated grassland (Fig. 4, Fig. S5); however, lack of modern resurvey data makes it difficult to estimate the proportion of habitat where invasion by exotic annual vegetation has resulted in extirpation. Historical resurveys are one of the best sources of information on how species have responded to climate and land-use change over the last century (Moritz et al., 2008; Stewart et al., 2015). Over two decades ago, Germano and Williams (1992) identified a status survey as top priority for *G. sila* recovery, noting that “no status survey has ever been conducted, even though the species was first federally listed in 1967.” These areas are long overdue for resurvey to determine if *G. sila* persists or has become extirpated.

Three previous studies used non-quantitative methods to estimate the proportion of *G. sila* habitat lost to development. They estimated that between 80–94% of habitat had been lost (Germano & Williams, 1992, 2005; Jennings, 1995). Based on our analysis of habitat lost to agriculture, development, and fragmentation (68% of habitat), discovery of apparent vegetation-climate mediated extirpations and range contraction, the large proportion of sites where *G. sila* have not been seen for decades, and other sources of unquantified habitat loss and degradation, we conclude that these previous estimates may reasonably bracket the proportion of habitat loss and range contraction experienced by the species. Other unquantified sources of habitat loss and degradation include off-road vehicle use, petrochemical extraction, solar infrastructure, and aerial application of insecticides (USFWS, 2010).

4.3. *Management implications*

Our results suggest that reclamation and restoration of endangered species habitat within the SJD may constitute a cost-effective strategy for recovery of dozens of threatened and endangered species. Under the anticipated climate scenario of increasing 21st-century drought conditions, the southern SJD valley floor may become too hot and dry for many of its endangered species (Appendix 1; Westphal et al., 2016). A prudent risk reduction strategy might involve increasing protected habitat in more mesic or northern portions of the SJD in the near term, before available lands are claimed for other uses (supplementary online text). We identify many areas of unconverted, apparently intact, SJD habitat where *G. sila* presence has not been documented for decades. We suspect that endangered species populations at many of these locations have succumbed to extirpation caused by the invasion of exotic grasses and forbs and by locally mesic climate conditions—a combination that results in prohibitively thick herbaceous vegetation. These areas are long overdue for resurvey to determine if endangered species populations have persisted. This type of range-wide status survey is an essential component of an endangered species protection and recovery program.

References

AghaKouchak A., Cheng L., Mazdiyasni O., & Farahmand A. (2014) Global warming and changes in risk of concurrent climate extremes: insights from the 2014 California drought. *Geophysical Research Letters*, **41**, 8847–8852.

Alexandratos N. & Bruinsma J. 2012. World agriculture towards 2030/2050: the 2012 revision. ESA Working Paper No. 12-03. *United Nations Food and Agriculture Organization*, Rome, Italy.

Ausubel J.H., Wernick I.K., & Waggoner PE. 2012. Peak Farmland and the Prospect for Land Sparing. *Population and Development Review*, **38**, 221–242.

Bailey C. V & Germano D.J. (2015) Probability of occupancy of blunt-nosed leopard lizards on habitat patches of various sizes in the San Joaquin Desert of California. *Western Wildlife*, **2**, 23–28.

Baillie J.E.M, Hilton-Taylor C., & Stuart S.N. 2004. 2004 IUCN red list of threatened species: a global species assessment. *International Union for the Conservation of Nature Species Survival Commission*, Gland, Switzerland and Cambridge, UK. Available from http://www.iucnredlist.org.

Bean W.T., Prugh L.R., Stafford R., Butterfield H.S., Westphal M., & Brashares J.S. (2014) Species distribution models of an endangered rodent offer conflicting measures of habitat quality at multiple scales. *Journal of Applied Ecology*, **51**, 1116–1125.

Bonn A., Schröder B., & Bonn A. (2001) Habitat models and their transfer for single and multispecies groups: a case study of carabids in an alluvial forest. *Ecography*, **24**, 483–496.

Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.* Springer, New York, NY.

CDFA (California Department of Food and Agriculture). 2013. California agricultural statistics review. *State of California*, Sacramento, CA.

Chauvenet A.L.M., Ewen J.G., Armstrong D.P., Blackburn T.M., & Pettorelli N. (2013) Maximizing the success of assisted colonizations. *Animal Conservation*, **16**, 161–169.

Cismowski G., Cooley W., Grober L., Martin J., McCarthy M., & Schnagl R. (2006) Salinity in the Central Valley. *Central Valley Regional Water Quality Control Board*, Rancho Cordova, CA.

Crooks J.A. (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Ecoscience*, **12**, 316–329.

Cypher B.L., Phillips S.E., & Kelly P.A. (2013) Quantity and distribution of suitable habitat for endangered San Joaquin kit foxes: conservation implications. *Canid Biology and Conservation*, **16**, 25–31.

Diffenbaugh N.S., Swain D.L., & Touma D. (2015) Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences*, **112**, 3931–3936.

Dzialowski E.M. (2005) Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology*, **30**, 317–334.

FAO (Food and Agriculture Organization of the United Nations). 2017. FAOSTAT. http://www.fao.org/faostat/ Accessed 10 April 2017.

Foley, J.A., DeFries R., Asner G.P., Barford C., Bonan G., Carpenter S.R., Chapin F.S., Coe M.T., Daily G.C., Gibbs H.K., Helkowski J.H., Holloway T., Howard E.A., Kucharik C.J., Monfreda C., Patz J.A., Prentice I.C., Ramankutty N., & Snyder P.K. 2005. Global Consequences of Land Use. *Science*, **309**, 570–574.

Funk W.C., McKay J.K., Hohenlohe P.A., & Allendorf F.W. (2012) Harnessing genomics for delineating conservation units. *Trends in Ecology and Evolution*, **27**, 489–496.

Germano D.J. & Rathbun G.B. (2016) Home range and habitat use by blunt-nosed leopard lizards in the southern San Joaquin Desert of California. *Journal of Herpetology*, **50**, 429–434.

Germano D.J., Rathbun G.B., Saslaw L.R., Cypher B.L., Cypher E.A., & Vredenburgh L.M. (2011) The San Joaquin Desert of California: ecologically misunderstood and overlooked. *Natural Areas Journal*, **31**, 138–147.

Germano D.J. & Williams D.F. (1992) Recovery of the blunt-nosed leopard lizard: paste efforts, present knowledge, and future opportunities. *Transactions of the Western Section of the Wildlife Society*, **28**, 38–47.

Germano D.J. & Williams D.F. (2005) Population ecology of blunt-nosed leopard lizards in high elevation foothill habitat. *Journal of Herpetology*, **39**, 1–18.

Goldingay R.L., Kelly P.A., & Williams D.F. (1997) The kangaroo rats of California: endemism and conservation of keystone species. *Pacific Conservation Biology*, **3**, 47–60.

Griffin D. & Anchukaitis K.J. (2014) How unusual is the 2012–2014 California drought? *Geophysical Research Letters*, **41**, 9017–9023.

Grimes A.J., Corrigan G., Germano D.J., & Smith P.T. (2014) Mitochondrial phylogeography of the endangered blunt-nosed leopard lizard, *Gambelia sila*. *Southwestern Naturalist*, **59**, 38–46.

Hanak E., Lund J., Arnold B., Escriva-bou A., Gray B., Green S., Harter T., Howitt R., Macewan D., Medellín-azuara J., Moyle P., & Seavy N. (2017) Water Stress and a Changing San Joaquin Valley. *Public Policy Institute of California*, San Francisco, CA, USA.

Harris J.A., Hobbs R.J., Higgs E.S., & Aronson J. (2006) Ecological restoration and global climate change. *Restoration Ecology*, **14**, 170–176.

Hawkins B.A., Field R., Cornell H.V., Currie D.J., Guégan J.-F., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O'Brien E.M., Porter E.E., & Turner J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hengl T., Jesus J.M. De, Macmillan R.A., Batjes N.H., Heuvelink G.B.M., Ribeiro E., Samuel-rosa A., Kempen B., Leenaars J.G.B., Walsh M.G., & Gonzalez M.R. (2014) SoilGrids1km: global soil information based on automated mapping. *PloS ONE*, **9**, e105992.

Jennings M.R. (1995) *Gambelia sila*. *Catalogue of American Amphibians and Reptiles*, **612**, 1–4.

Kelly P.A., Phillips S.E., & Williams D.F. (2005) Documenting ecological change in time and space: the San Joaquin Valley of California. *Mammalian Diversification: From Chromosomes to Phylogeography (A Celebration of the Career of James L. Patton)* (ed. by J.L. Patton, E.A. Lacey, and P. Myers), pp. 57–78. University of California Press, Berkley, CA.

Kramer-Schadt S., Niedballa J., Pilgrim J.D., Schröder B., Lindenborn J., Reinfelder V., Stillfried M., Heckmann I., Scharf A.K., Augeri D.M., Cheyne S.M., Hearn A.J., Ross J., Macdonald D.W., Mathai J., Eaton J., Marshall A.J., Semiadi G., Rustam R., Bernard H., Alfred R., Samejima H., Duckworth J.W., Breitenmoser-Wuersten C., Belant J.L., Hofer H., & Wilting A. (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions*, **19**, 1366–1379.

Laymon S., Olsen B., Kraft K., Lair K., Hult S., & Touré T. (2010) Atwell Island Restoration Project activities 2000-2010. *U.S. Department of the Interior Interagency Land Retirement Team*, Fresno, CA.

Means D.B. (1975) Competitive exclusion along a habitat gradient between two species of salamanders (*Desmognathus*) in western Florida. *Journal of Biogeography*, **2**, 253–263.

Melton F., Rosevelt C., Guzman R., Johnson L., Zaragoza I., Thenkabail P., Wallace W., Mueller R., Willis P., Jones J., & Verdin J. (2015) Fallowed area mapping for drought impact reporting: 2015 assessment of conditions in the California Central Valley. *NASA Ames Research Center*, Mountain View, CA.

Mills L.S. & Allendorf F.W. (1996) The one migrant per generation rule in conservation and management. *Conservation Biology*, **10**, 1509–1518.

Montanucci R.R. (1965) Observations on the San Joaquin Leopard Lizard, *Crotaphytus wislizenii silus* Stejneger. *Herpetologica*, **21**, 270–283.

Montanucci R.R. (1967) Further studies on leopard lizards, *Crotaphytus wislizenii*. *Herpetologica*, **23**, 119–126.

Moritz C., Patton J.L., Conroy C.J., Parra J.L., White G.C., & Beissinger S.R. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, **322**, 261–264.

Nelson C., Lasagna B., Holtgrieve D., & Quinn M. (2003) The Central Valley historic mapping project. *Chico State Geographical Information Center*, Chico, CA.

Olmstead A.L. & Rhode P.W. (2003) The evolution of California agriculture: 1850-2010.

California Agriculture: Dimensions and Issues (ed. by J. Siebert), pp. 1–28. University of California, Giannini Foundation of Agricultural Economics, Davis, CA.

Pearce D., Young S., Wesolowski G., Cowan J., & Gwin A. (2015) San Joaquin Valley landscape-scale planning for solar energy and conservation. Unpublished Master's Thesis. *Bren School of Environmental Science and Management*, University of California, Santa Barbara, CA.

Peters G.P., Andrew R.M., Boden T., Canadell J.G., Ciais P., Quéré C. Le, Marland G., Raupach M.R., & Wilson C. (2013) The challenge to keep global warming below 2°C. *Nature Climate Change*, **3**, 4–6.

Pierce D.W., Das T., Cayan D.R., Maurer E.P., Snyder M.A., Sloan L.C., Franco G., & Tyree M. (2013) Probabilistic estimates of future changes in California temperature and precipitation using statistical and dynamical downscaling. *Climate Dynamics*, 839–856.

Prugh L.R. & Brashares J.S. (2012) Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. *Journal of Animal Ecology*, **81**, 667–678.

Queiroz C., Beilin R., Folke C., & Lindborg R. 2014. Farmland abandonment: Threat or opportunity for biodiversity conservation? A global review. *Frontiers in Ecology and the Environment*, **12**, 288–296.

Richmond J.Q., Wood D.A., Westphal M.F., Vandergast A.G., Leaché A.D., Saslaw L.R., Butterfield H.S., & Fisher R.N. (2017) Persistence of historical population structure in an endangered species despite near-complete biome conversion in California's San Joaquin Desert. *Molecular Ecology*, available early online. DOI: 10.1111/mec.14125

Schoups G., Hopmans J.W., Young C.A., Vrugt J.A., Wallender W.W., Tanji K.K., & Panday S. (2005) Sustainability of irrigated agriculture in the San Joaquin Valley, California. *Proceedings of the National Academy of Sciences*, **102**, 15352–15356.

Schulman L., Toivonen T., & Ruokolainen K. (2007) Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *Journal of Biogeography*, **34**, 1388–1399.

Shumway C.R. (1973) Derived demand for irrigation water: the California Aqueduct. *Journal of Agricultural and Applied Economics*, **5**, 195–200.

Sinervo B., Méndez-de-la-Cruz F., Miles D.B., Heulin B., Bastiaans E., Villagrán-Santa Cruz M., Lara-Resendiz R., Martínez-Méndez N., Calderón-Espinosa M.L., Meza-Lázaro R.N., Gadsden H., Avila L.J., Morando M., De la Riva I.J., Victoriano Sepulveda P., Rocha C.F.D., Ibargüengoytía N., Aguilar Puntriano C., Massot M., Lepetz V., Oksanen T.A., Chapple D.G., Bauer A.M., Branch W.R., Clobert J., & Sites J.W. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science*, **328**, 894–9.

Stewart J.A.E., Perrine J.D., Nichols L.B., Thorne J.H., Millar C.I., Goehring K.E., Massing C.P., & Wright D.H. (2015) Revisiting the past to foretell the future: summer temperature and habitat area predict pika extirpations in California. *Journal of Biogeography*, **42**, 880–890.

Strayer D.L., Eviner V.T., Jeschke J.M., & Pace M.L. (2006) Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution*, **21**, 645–651.

Syfert M.M., Smith M.J., & Coomes D.A. (2013) The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS ONE*, **8**, e55158.

Tallmon D.A., Luikart G., & Waples R.S. (2004) The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology and Evolution*, **19**, 489–496.

Udall S.L. (1967) Native fish and wildlife: endangered species. *Federal Register*, **34**, 4001.

United States Fish and Wildlife Service [USFWS] (2010) Blunt-nosed leopard lizard (*Gambelia sila*) 5-year review: summary and evaluation. United States Fish and Wildlife Service. Sacramento, CA.

Wang S. & Hipps L. (2014) Probable causes of the abnormal ridge accompanying the 2013–2014 California drought: ENSO precursor and anthropogenic warming footprint. *Geophysical Research Letters*, **41**, 3220–3226.

Webb W., Szarek S., Lauenroth W., Kinerson R., & Smith M. (1978) Primary productivity and water use in native forest, grassland, and desert ecosystems. *Ecology*, **59**, 1239–1247.

Wester L. (1981) Composition of native grasslands in the San Joaquin Valley, California. *Madrono*, **28**, 231–241.

Westphal M.F., Stewart J.A.E., Tennant E.N., Butterfield H.S., & Sinervo B. (2016) Contemporary drought and future effects of climate change on the endangered blunt-nosed leopard lizard, *Gambelia sila*. *Plos One*, **11**, e0154838.

Williams D.F., Cypher E.A., Kelly P.A., Miller K.J., Norvell N., Phillips S.F., Johnson C.D., & Colliver G.W. (1998) Recovery plan for upland species of the San Joaquin Valley, California. *U.S. Fish and Wildlife Service*, Portland, OR.

Data Accessibility Statement

All habitat suitability models generated for this study are available as raster grids from Data Basin, https://databasin.org/.

Biosketch

Joseph Stewart is a PhD candidate at the University of California Santa Cruz. His research focuses on understanding the patterns and processes of ongoing biodiversity declines—with the goal of developing cost-effective solutions for effective stewardship of our diverse natural heritage. Currently, his favorite San Joaquin Desert wildflower is *Salvia carduacea*.

Tables

Table 1. Performance metrics and variable contribution of top performing habitat suitability models. Performance metrics are AICc model weight (W), change in Akaike's information criterion (ΔAICc), area under the receiver operating characteristic curve (AUC), Boyce Index (BI), and unregularized training gain (Gain). Models are ranked in order of increasing ΔAICc. See Table S3 for variable abbreviations and definitions. Blank cells indicate a variable was not included in the model. (A) The top five performing models selected from all 236 candidate models. Satellite derived vegetation productivity (NDVI) is the top predictor of *G. sila* distribution, however because NDVI is modified by agriculture it is not an appropriate predictor of historical, paleontological, or future distribution. (B) The top five performing models selected from the 197 candidate models that do not include NDVI. The top two performing models from B are the sixth and seventh ranked models (ΔAICc = [40.064, 42.194]) from the full set of 236 candidate models.

	Performance Metric					**% Variable Contribution**										
	W	ΔAICc	AUC	BI	Gain	slope	NDVI	AET	CWD	MAP	pH	clay	EC	h_r	h_a	dipo
A	0.853	0.000	0.931	0.987	1.414	15.5	55.6					5.7	0.5	22.7		
	0.147	3.517	0.930	0.991	1.404	14.5	56.6					5.5		23.3		
	0.000	30.986	0.929	0.989	1.384	17.9	67.2					7.6	0.3		6.9	
	0.000	34.660	0.928	0.995	1.378	17.2	66.2					7.9			6.5	2.2

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	0.000	36.930	0.927	0.991	1.370	17.5	67.3					7.9			7.2	
	W	ΔAICc	AUC	BI	Gain	slope	NDVI	AET	CWD	MAP	pH	clay	EC	h_r	h_a	dipo
B	0.743	0.000	0.926	0.951	1.368	6.4				86.4	2.5	3.7	0.9			
	0.256	2.130	0.926	0.947	1.366	10.4		77.5			7.2	3.8	1.0			
	0.001	13.406	0.924	0.941	1.350			80.7			11.8	3.3	1.9			2.2
	0.000	17.522	0.923	0.982	1.348	10.5		79.6			4.8		2.5			2.6
	0.000	17.950	0.923	0.809	1.343	7.3				47.1	2.7	4.2			38.7	

Figures

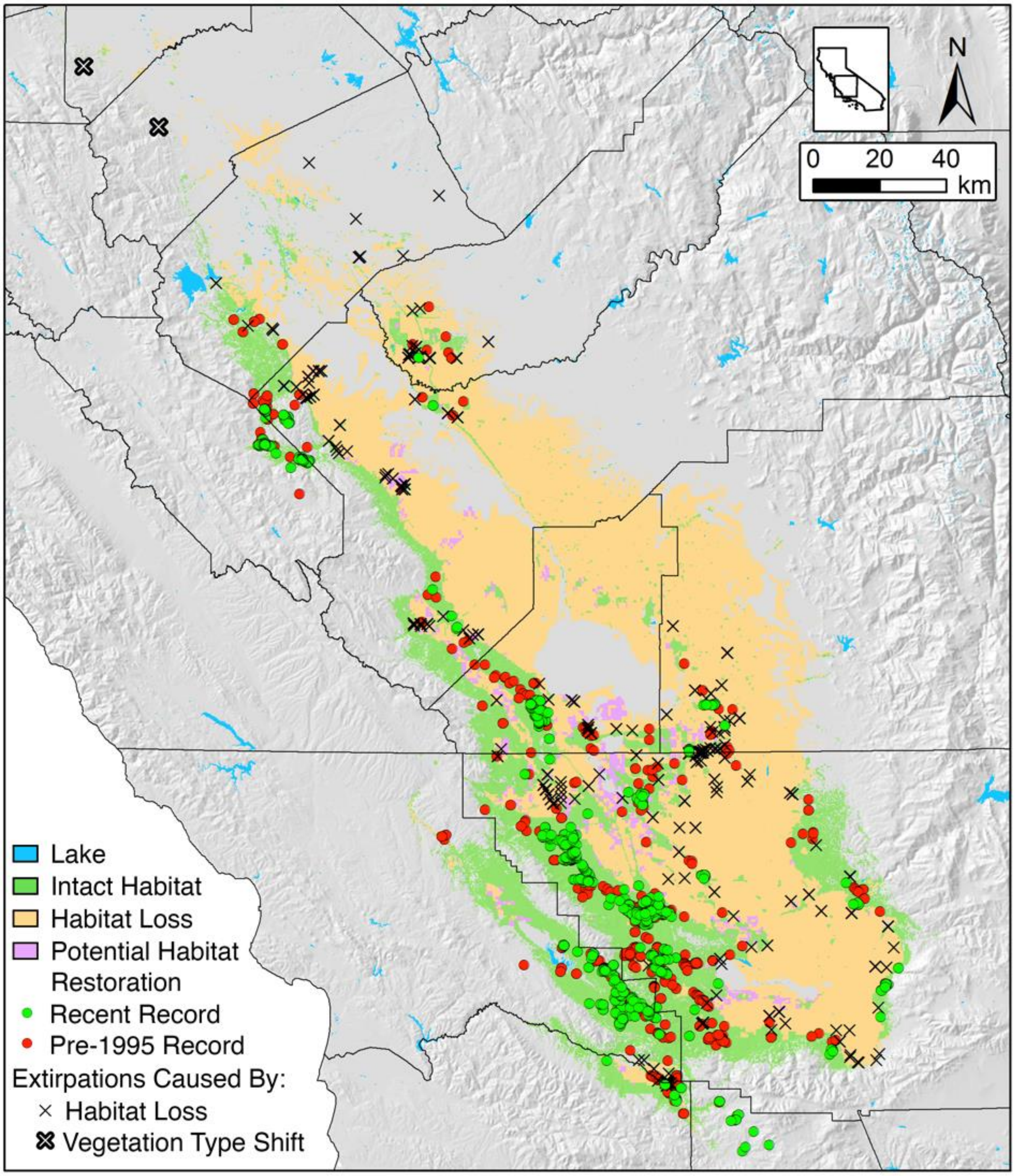

Fig 1. The historical distribution of habitat for our SJD umbrella species, *G. sila*, extant sites, extirpated sites, lost habitat, and sites where persistence of *G. sila* has not been confirmed since before 1995. Extirpations caused by vegetation type shifts are sites apparently extirpated due to dense exotic vegetation. Areas of potential habitat restoration are sites that were continuously fallow (2013–2015) and, if restored, would constitute of a patch of habitat of sufficient size to have a ≥ 90% probability of long term population persistence. County boundaries are shown in black.

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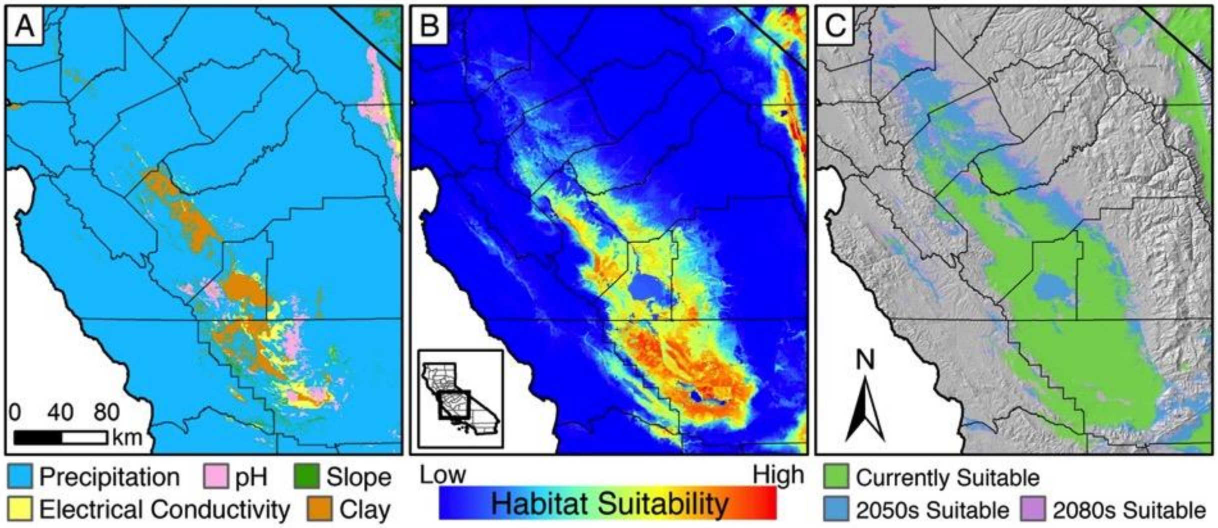

Fig 2. (A) Limiting environmental covariates across geographic space for our umbrella species, *G. sila*, assessed using the top-performing model of habitat quality and in absence of anthropogenic impacts. High precipitation, and resulting high herbaceous vegetation biomass, are the most limiting variables for the lizard (see Table S3 for variable definitions). **(B)** Continuous ensemble habitat suitability over the geographic range of *G. sila*. High clay content, acidic, and overly saline soils create pockets of low and non-suitable habitat within the range of the lizard. **(C)** Projected climate-driven expansion of suitable habitat for *G. sila* under anticipated drought conditions (MIROC-ESM, RCP8.5). By 2050, suitable habitat is projected to expand northward to include previously occupied sites at the species' former northern range margin. Also by 2050, a corridor of newly suitable habitat connects the southeastern terminus of the range of blunt-nosed leopard lizards, *G. sila*, with the range of long-nosed leopard lizards, *G. wislizenii*.

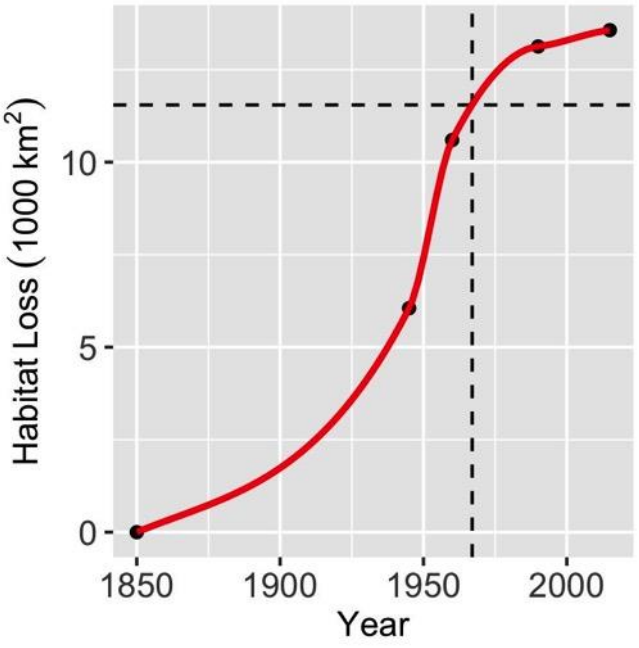

Fig 3. Area of *G. sila* habitat converted to agricultural and urban development over time as estimated from the intersection of historical land use maps and predicted historical distribution. Dashed lines correspond to the year 1967, when the species was protected under the federal ESA.

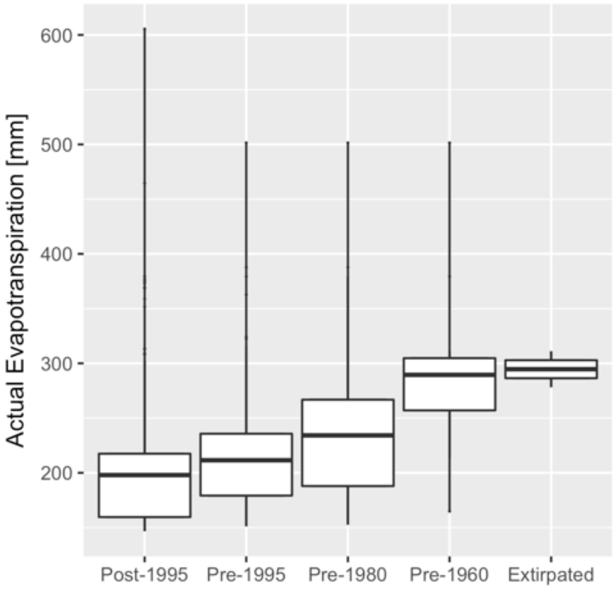

Fig. 4. Actual evapotranspiration (AET) at *G. sila* record locations on undeveloped habitat is higher at sites where *G. sila* has not been seen for longer and where *G. sila* is now extirpated (Kruskal-Wallis rank sum test, $P < 10^{-14}$). Shown are AET values at unique locations where *G. sila* were detected only within the given range of years (5-km radius). Extirpated sites are historical record locations that were surveyed extensively to confirm loss of lizard populations (Fig. 1). Boxes and whiskers depict the mean, interquartile range, and range.

Additional supplementary information may be found in the online version of this article:

Appendix 1. Habitat conservation priorities in the San Joaquin Desert.
Appendix 2. Impacts of climate change.
Table S1. Threatened and endangered species of the San Joaquin Desert.
Table S2. Biases and critiques of previous species distribution models.
Table S4. Resurveys at apparently extirpated record locations.
Table S5. Locations of recent habitat destruction.
Table S6. Locations of *Gambelia sila* occurrence observed on retired agricultural lands.
Fig. S1. Hours of restriction and hours of activity for *Gambelia sila*.
Fig. S2. Performance of candidate umbrella species.
Fig. S3. Density plots for candidate predictor variables.
Fig. S4. Habitat suitability in Westlands Water District.
Fig. S5. Change in climatic niche of *Gambelia sila* over time.