# EVALUATING CURRENT AND FUTURE RANGE LIMITS OF AN ENDANGERED, KEYSTONE RODENT (*DIPODOMYS INGENS*)

By

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# ABSTRACT

## EVALUATING CURRENT AND FUTURE RANGE LIMITS OF AN ENDANGERED, KEYSTONE RODENT (*DIPODOMYS INGENS*)

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Climate is often considered the single most important factor limiting species' ranges. Other factors, such as biotic interactions, are often assumed to be included via abiotic proxies. However, differential responses to climate change may decouple these relationships or lead to adaptation to novel environments. Accounting for competition and local adaptation should more accurately describe environmental factors influencing current distributions and increase the predictive accuracy of future distributions. Modeling the endangered giant kangaroo rat (*Dipodomys ingens*) is an excellent application of these model improvements, as the species range consists of geographically and genetically isolated populations experiencing disparate climatic change. From eight years of trapping data, I used Maxent to model the distributions of two isolated populations of *D. ingens*. Using local surveys and state-wide data, I also modeled California ground squirrels (*Otospermophilus beecheyi*), a potential novel competitor. Models included landscape variables (slope and soil composition) and climate variables (temperature, precipitation, and climatic water deficit). Niche overlap between the *D. ingens* populations was moderate ($I = 0.43$), suggesting that they already experience different climatic regimes and providing support for population-level modeling.

Projecting population models into the future, under a high emission climate change scenario (CCSM4, rcp8.5), resulted in less predicted range contraction than modeling the species as a whole. However, forecasted distributions showed areas of increasing niche overlap between the Panoche population of *D. ingens* and *O. beecheyi* ($I$ = 0.63 to 0.74), indicating competition could be a novel range limit. These species distribution models identify range limiting factors and detect potentially important future habitat. However, 27% of modeled suitable habitat is currently in agricultural use, preventing *D. ingens* occupation. In combination with historical distribution models, we can target key areas to prevent further anthropogenic development and to protect the giant kangaroo rat within an endangered ecosystem.

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# INTRODUCTION

Climate is often considered the single most important factor limiting species' ranges (e.g. Merriam 1894, Peterson 2011). Most contemporary approaches to modeling species distributions and predicting range shifts under climate change suggest species will relocate to track their climatic niches (Parmesan 2006). This response is governed by niche conservatism, which occurs when species retain ecological traits related to their niche over time (Wiens et al. 2010). Throughout the text, "niche" refers to the combination of abiotic and biotic factors that a species experiences and their distribution in geographic space (Hutchinson 1957). Niche conservatism suggests that species maintain their relationship with environmental factors, even in the absence of those niche characteristics. Thus, species may shift their range through space to follow the conditions to which they are adapted, or they may locally express retained traits in response to change. The interaction between abiotic and biotic factors is important in determining whether species follow or deviate from niche conservatism.

Abiotic factors, often related to climate and topography, are commonly used in distribution and niche modeling (e.g. Lawler et al. 2006, Escalante et al. 2013, Aycrigg et al. 2015, Beaumont et al. 2016). While some large-scale studies have detected movements poleward or toward higher elevations (e.g. Parmesan and Yohe 2003), long-term and fine-scale studies have revealed more idiosyncratic responses to climate change (e.g. Moritz et al. 2008, Gibson-Reinemer and Rahel 2015). Species, or even populations, respond inconsistently to climatic changes; some shift their range across latitude or longitude, some shift in elevation, and others remain stable (Gibson-Reinemer and Rahel 2015). This is often explained by geographically tracking temperature and retaining niche characteristics.

Climate-driven models of species distributions have received criticism for focusing on temperature without consideration of precipitation (Rapacciulo et al. 2014). While temperature is vital in determining local climate, precipitation also plays a large role by shaping the vegetative community. Community structure directly affects primary productivity, a major limiting factor for many species (Brown et al. 1979). Tingley et al. (2009) compared niche shifts of 53 bird species from historical (1911-1929) to contemporary (2003-2008), showing that species' responses to changing climate could not be predicted solely from temperature or precipitation, but estimates were far more accurate when the two were used in tandem.

Even with the improved accuracy from multiple climatic variables, broad correlations between species distributions and climate may obscure local adaptations. Species ranges may shift to track a fluctuating niche, but others remain in place, exposing them to changes in climate (Holt 1990). Noncontiguous populations within a species could experience dissimilar climatic conditions, and over time the population-level niche could vary based on local conditions (Gibson-Reinemer and Rahel 2015). Including multiple aspects of climate may make predictions more accurate, but still neglects the potentially powerful influence of biotic interactions, such as competition.

Competition limits resource use when competing species co-occur in small areas and can serve as a range limit where geographic ranges meet (Boulangeat et al. 2012).

Biotic interactions are governed by niche overlap and/or geographic overlap of multiple species. Small mammal communities are structured by internal mechanisms to avoid competition (e.g. microhabitat partitioning, resource selection, temporal separation) (Price 1978). While these processes may reduce the effects of competition within communities, the boundaries between communities could serve as intense areas of competition, which can influence species distributions (Gaston 2003). Even niche partitioning within a community does not prevent interspecific competition (e.g. Hughes et al. 1994). Climate change is expected to affect community assembly, with species expanding across community boundaries at different rates, inducing novel competitive interactions (Montoya and Raffaelli 2010). Antagonistic interactions become potential limits to distribution, as competitors could prevent range expansion of less dominant or more specialized species (Lurgi et al. 2012). Most species distribution models – whether explicitly stated or not – incorporate biotic interactions through indirect abiotic proxies, such as attempting to capture competitive species boundaries with differences in temperature (Guisan and Thuiller 2005). However, because species respond to climate change at various scales and via different mechanisms, the relationship between climate and competition may be decoupled when projecting into the future (Guisan and Thuiller 2005, Elith and Leathwick 2009, Lurgi et al. 2012). Consideration of biotic limitations directly may better explain the mechanisms limiting current distributions and, therefore, more accurately forecast species distributions under future climates.

The giant kangaroo rat (*Dipodomys ingens*) is an ideal species to test the inclusion of local adaptation and biotic interactions into species distribution modeling. They are a state and federally listed endangered species endemic to California's San Joaquin Valley (USFWS 1987). They currently only reside in a few remnant, and often isolated populations, the largest of which are found in the Carrizo Plain National Monument (Carrizo) and the Ciervo-Panoche Natural Area (Panoche). These two populations are geographically isolated by about 150 km, and recent work suggests genetic isolation dating back at least 10,000 years (Statham et al. In review), making local adaptation more likely (CDFW 2016). Although populations may experience different local conditions, the species exists within a narrow range of habitat characteristics (Bean et al. 2014a). These habitat specialists thrive in desert-grasslands with low annual precipitation, (< 30 cm), sandy loam soils, and flat or very low-grade slopes, particularly below six degrees (Grinnell 1932, Hawbecker 1951, and Bean et al. 2014a). Their burrow structures are used by other vertebrate species, including some classified as endangered, and their seed caching may serve as a food source for invertebrate inhabitants (Prugh and Brashares 2012). They are thus thought to be ecosystem engineers and, due to their impact despite generally low abundance, a keystone species (Prugh and Brashares 2012). Understanding the limitations to *D. ingens* range should aid in crafting more effective conservation strategies, and help protect an endangered ecosystem.

Precipitation appears to play a key role in limiting *D. ingens* distributions (Bean et al. 2014a). Persistence in areas of low annual precipitation is presumably limited by food resources, particularly after consecutive years of low rainfall. However, the specific mechanisms by which precipitation limits *D. ingens* in the wetter parts of their range is undetermined (Bean 2012). *D. ingens* could be limited by precipitation in several ways, leading to three non-exclusive mechanistic hypotheses.

### The Precipitation Hypothesis

As a burrowing, seed-caching species, high precipitation could directly affect their ability to maintain burrows, or cause seed spoilage, depleting seasonal food stores (Valone et al. 1995). In this case, excess precipitation would limit the geographic range. Conversely, areas of insufficient precipitation may not support adequate food resources, again limiting geographic range (Figure 1).

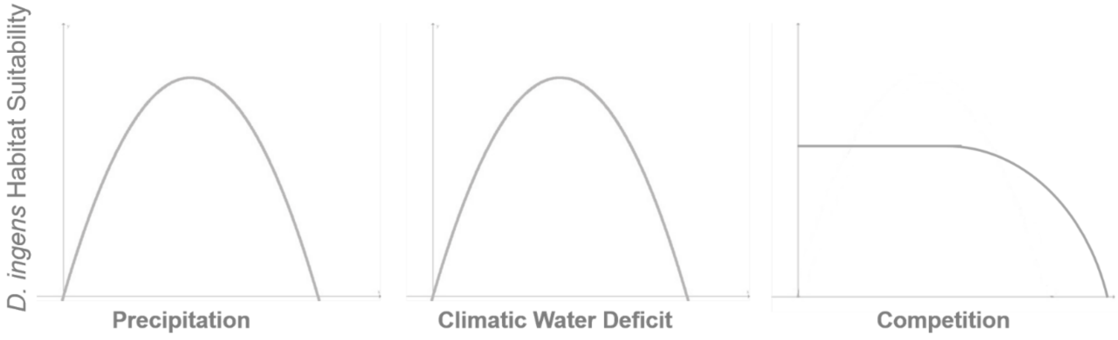

Figure 1. Expected relationships between range-limiting variables and habitat suitability for giant kangaroo rats (*Dipodomys ingens*). Relationships reflect the three hypotheses presented in the text.

### The Vegetation Hypothesis

Higher precipitation causes increased growth of dense, non-native vegetation (e.g. *Bromus madritensis* spp. *rubens*) that impedes *D. ingens* movement, decreasing foraging efficiency and increasing the risk of predation (Germano et al. 2012). Precipitation may variably affect plant growth according to local environmental conditions and the availability of water post-rainfall. Climatic water deficit is the amount of evapotranspiration that would have occurred, given more water in the system. It combines the effects of precipitation, temperature, and radiation to provide a metric of available water that helps shape the identity of the vegetative community. A lower deficit would result in increased soil moisture, which could improve growth conditions for dense non-native vegetation, inhibiting saltatorial movements (Stephenson 1998). Conversely, a greater deficit could prevent primary productivity altogether, limiting the food supply (Figure 1).

## The Competition Hypothesis

As the largest of the kangaroo rat species, *D. ingens* is considered competitively dominant within its community, which includes other *Dipodomys* species (Grinnell 1932, Prugh and Brashares 2012, Bean 2012). *D. ingens* adapted to thrive in extremely arid regions, and maintains dominance over similarly-sized or smaller species. However, wetter areas of their range are suitable to potential novel competitors, increasing the possibility for a loss of the competitive dominance of *D. ingens* (Figure 1). Populations in areas of higher precipitation have a greater chance of interacting with California ground squirrels (*Otospermophilus beecheyi*) which currently occupy the fluctuating wetter edges of *D. ingens* habitat. Direct contact between species could result in antagonistic interactions, as *O. beecheyi* is known to be aggressive (Trulio 1996). In fact, Williams and Germano (1993) observed *O. beecheyi* raiding *D. ingens* seed caches and have anecdotal evidence of a direct mortality or eviction event of *D. ingens* due to burrow invasion. Additionally, *O. beecheyi* is a diet and habitat generalist that has shown little response to climate change over the last century and could pose a threat to *D. ingens* expansion into wetter territory (Grinnell and Dixon 1918, Moritz et al. 2008, Eastman et al. 2012, Hubbart 2012).

The Carrizo and Panoche *D. ingens* populations appear to be genetically isolated (Statham et al. in Review) and experience different climatic regimes – the Panoche, receives up to over 10 cm (~45%) more average annual precipitation than Carrizo. It is therefore possible that the two populations of *D. ingens* respond differently to increasing levels of precipitation and, over time, adapted to their respective local conditions. A distribution model of the Panoche population would incorporate areas of higher precipitation than that of the Carrizo population. This could reduce niche overlap between populations, but predict less range contraction given the populations are adapted to a wider range of climatic conditions.

I tested three hypotheses of *D. ingens* range limitation, which I tested by identifying important variables in species distribution models. By incorporating more direct mechanisms – i.e., local adaptation and biotic interactions -- I attempted to improve the predictive accuracy of habitat suitability from species distribution models for *D. ingens*. I created a suite of distribution models using Maxent including: (1) rangewide *D. ingens*, (2) population specific *D. ingens* in the Panoche, (3) population specific *D. ingens* in the Carrizo, and the same set of models for *O. beecheyi* (4-6). To test the efficacy of the models including local adaptation, I compared the rangewide model (1) to the population-level niche models (2 and 3) to determine differences of population-level models. Then, I used the Panoche and Carrizo models to project the population-level estimates of habitat suitability rangewide, for both current and future climate. Finally, I estimated niche overlap between *D. ingens* and *O. beecheyi* to assess the possibility of a competitive interaction limiting *D. ingens* range expansion. To inform future management, I projected the top performing models into the future.

# STUDY AREA

The San Joaquin Valley, the southern portion of California’s Central Valley, is a desert grassland characterized by mild winters with low rainfall, and hot, dry summers. The vegetative community includes primarily annual grasses and forbs as well as some perennial shrubs (Germano et al. 2011). Much of the land, particularly in the eastern portion of the valley, primarily includes agriculture that has replaced *D. ingens* habitat (Williams et al. 1998). Land converted to agriculture is tilled and irrigated making it unsuitable to *D. ingens*. After conversion to agriculture, the next greatest threat to persistence within remaining *D. ingens* populations is land conversion for solar energy development (USFWS 2010).

The northern population of *D. ingens* persists in the Ciervo-Panoche Natural Area (Panoche) in San Benito and Fresno Counties (Figure 2). While this population’s habitat is the more mesic of the two, mean annual rainfall is still low (~20-30 cm). *D. ingens* are sparsely distributed on the locally available areas of level terrain as well as gradual slopes. Soil composition in this area is dominated by sand, but smaller particles of silt and clay are present in significant quantities (NRCS 2003).

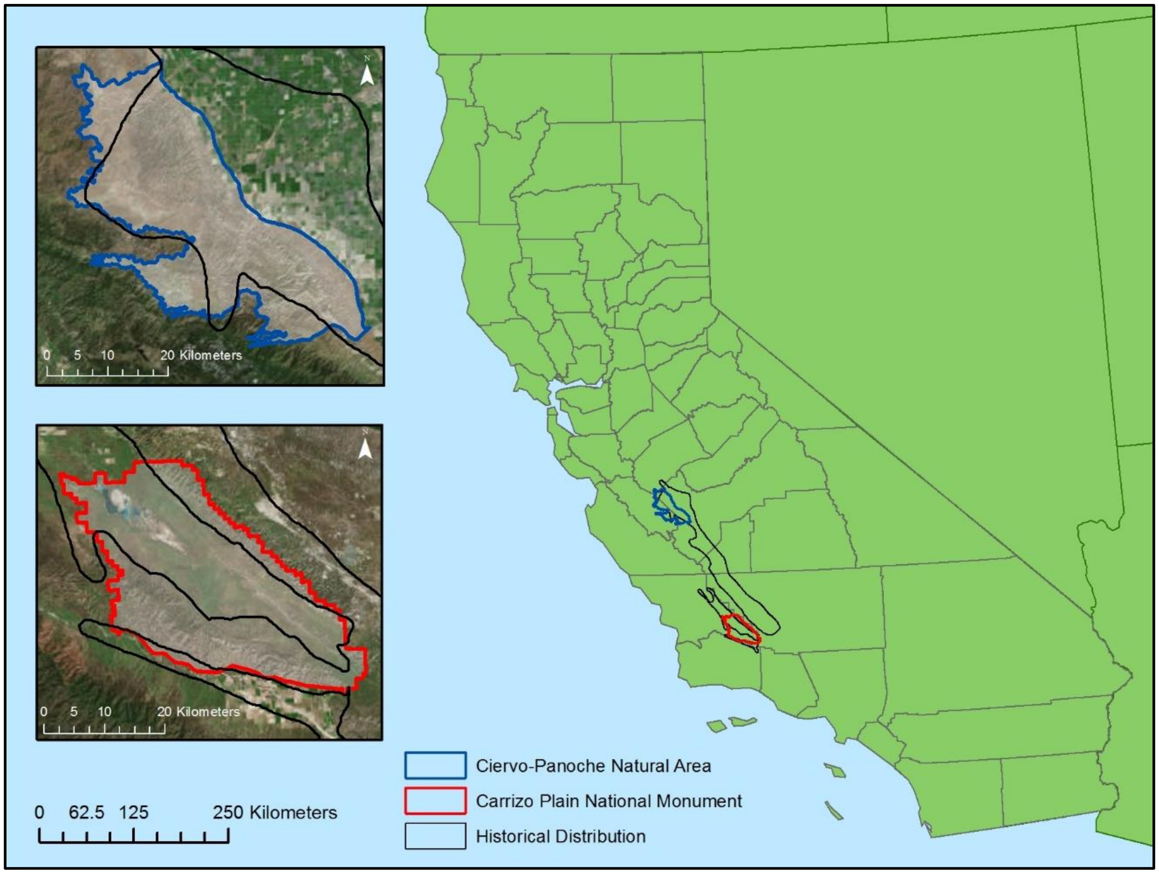

Figure 2. Study area including the Ciervo-Panoche Natural Area (top left image, North on map) in San Benito and Fresno Counties, California, and the Carrizo Plain National Monument (bottom left image, South on map) in San Luis Obispo County, California. The black outline indicates the historical distribution presented by Williams et al. (1992).

Much like in the Panoche, the Carrizo population of *D. ingens* has faced habitat loss due to conversion for agriculture and oil development in the surrounding area. The Carrizo has served as an area of refuge for endemic species, including rare and endangered plants and animals (Buck-Diaz and Evans 2011). The landscape is characterized by grasslands and ridges, as well as Soda Lake, a natural alkali wetland. Mean annual rainfall is lower than in the Panoche, at approximately 17-23cm per year (California Department of Water Resources 2004). Although variable across the landscape, soil composition here is generally higher in sand, with fewer smaller particles than the Panoche, potentially restricting *D. ingens* to shorter, less complex burrow systems (Laundré and Reynolds 1993, NRCS 2003).

In California, the average annual temperature increased 1.7$^{o}$C over the last century, which is 70% higher than the national average increase (Moser et al. 2009). The state has experienced extended periods of drought, like the recent D4 (exceptional drought) conditions in the Central Valley (National Drought Mitigation Center 2016). According to Cal-Adapt (2018), a compilation of climate research from various locations in California, the maximum temperature in the Panoche is expected to increase between 2.5 and 4.1°C by the years 2070-2099. Annual precipitation is expected to remain stable or to increase by up to 2.8 cm (Cal-Adapt 2018). The temperature in the Carrizo is predicted to increase by 1.8 to 3.4°C by the years 2070-2099, and precipitation is expected to decrease between 3 and 3.8 cm (Cal-Adapt 2018).

# METHODS

I used presence-only data derived from live-trapping and visual surveys to construct species distribution models for two species and to project suitability into the future. Live-trapping of *D. ingens* occurred in the summers of 2010 through 2017 (Bean et al. 2012, N. Alexander, unpublished data, and A. Semerdjian, unpublished data). All individuals were marked with a unique ear tag and morphological measurements were recorded. I conducted driving surveys and recorded opportunistic sightings of *O. beecheyi*. I established a suite of current species distribution models using climatic variables and other remotely sensed data and used projected climate conditions to create future models. Models for both populations (Panoche and Carrizo) and rangewide were constructed for *D. ingens* as well as for *O. beecheyi*. I then compared the niche overlap of the *D. ingens* populations and *O. beecheyi* now and in the future.

## Data Collection

### Live Trapping

Occurrence data came from eight years of both occupancy and grid trapping across the range. Both methods of trapping occurred in the Carrizo in 2010- 2017 (excluding 2013 and 2015), and in the Panoche in 2011-2017 (excluding 2012). This target-based trapping consisted of using extra-long Sherman live traps to identify presence of *D. ingens* at sites with occupancy signs, such as burrows mounds or scat. In the Panoche, each of the sites contained 5-20 traps placed near potentially occupied burrow openings. Trapping grids were 100m ×100m, with 61 traps spaced 20m apart and offset into a checkerboard pattern (Prugh and Brashares 2012). All traps were baited with millet, opened at dusk, and checked starting at midnight (Prugh and Brashares 2010, Alexander et al. In Review). I collected data during the summers of 2016 and 2017. In 2016, traps were set for five consecutive nights. Capture probability was high enough that three nights were sufficient to detect presence; therefore, in 2017 traps were only set for three consecutive nights.

Presence was noted upon the capture of an individual as well as traps considered "empty", "tripped" or "inoperable". Trap location was noted, but presence was identified at site level, including clusters of traps as well as grids. All animals were handled using exclusively physical restraint. I measured weight (grams) and noted the sex (male or female) and reproductive condition (scrotal, not scrotal, pregnant, lactating, post-lactation, not reproductive). Prior to 2017, animals with food in their cheek pouches were reweighed upon recapture or not considered when estimating weight. Recapture rates were high enough to allow for this method while excluding minimal data. In 2017, due to fewer trapping nights, seeds were manually pushed out of the cheek pouches into the handling bag to be subtracted from the total weight. Each new individual received a unique ear tag and recaptures were recorded and released.

All work was performed under Humboldt State Animal Care Protocol 13-14.W.109-A and 16/17.W.96-A and followed American Society of Mammalogists guidelines (Sikes et al. 2011).

### Environmental Variables

I acquired climatic data from the Basic Characterization Model (Flint and Flint 2014). I used a digital elevation model to calculate slope (USGS 2013) and used estimates of soil texture to incorporate important aspects of burrowing requirements (NRCS 2003). All environmental variables were resampled to the coarsest resolution for modeling, about 900 m (Table 1).

Table 1. Environmental variable layers that were included in the candidate model sets for species distribution models for *Dipodomys ingens* and *Otospermophilus beecheyi*. All variables were resampled to the coarsest resolution.

| **Layer Name** | **Environmental Variable** | **Relevance** | **Source** | **Spatial Resolution** | **Temporal Resolution** |
|---|---|---|---|---|---|
| precip | Mean annual **precipitation** | Forage Availability, Food Spoilage | Basin Characterization Model (Flint and Flint 2014) | 270m | 1981-2010 |
| cwd | Mean annual **climatic water deficit** | Forage Availability Locomotion | Basin Characterization Model (Flint and Flint 2014) | 270m | 1981-2010 |
| mintemp | Mean annual **minimum temperature** | Foraging Time, Forage Type | Basin Characterization Model (Flint and Flint 2014) | 270m | 1981-2010 |
| maxtemp | Mean annual **maximum temperature** | Foraging Time, Forage Type | Basin Characterization Model (Flint and Flint 2014) | 270m | 1981-2010 |
| sand | Mean percent **sand** in soil | Burrowing | Soil Survey Geographic Database (NRCS 2003) | 900m | 2003 |
| clay | Mean percent **clay** in soil | Burrowing | Soil Survey Geographic Database (NRCS 2003) | 900m | 2003 |
| slope | Degrees of **slope** | Burrowing, Locomotion | US Geologic Survey (USGS 2013) | 30m | 2013 |

## Driving Surveys

In 2017 I conducted driving surveys to record sightings of *O. beecheyi* within a 50 km radius of the Panoche (Figure 3). With an additional observer, I drove five survey routes ranging between 130 and 190 km. In order to survey a range of environmental conditions, the five routes were stratified into five equally binned current (1981-2010) precipitation zones (171-280 mm, 281-390 mm, 391-500 mm, 501-610 mm, 611-720 mm) and overall the survey contained approximately equal numbers of survey points among these precipitation zones (Flint and Flint 2014). I stopped every four km, according to a waypoint, and two observers used binoculars to search for *O. beecheyi* for two minutes (Downey 2003). If a squirrel was detected before the two minutes were complete, the point was coded as a presence and the survey continued. If no squirrels were seen within two full minutes, the site was coded as no apparent presence and the survey continued. Opportunistic sightings during the surveys and during *D. ingens* trapping were also recorded. Each route was sampled once during 2017, and surveys occurred on separate days from June to July.

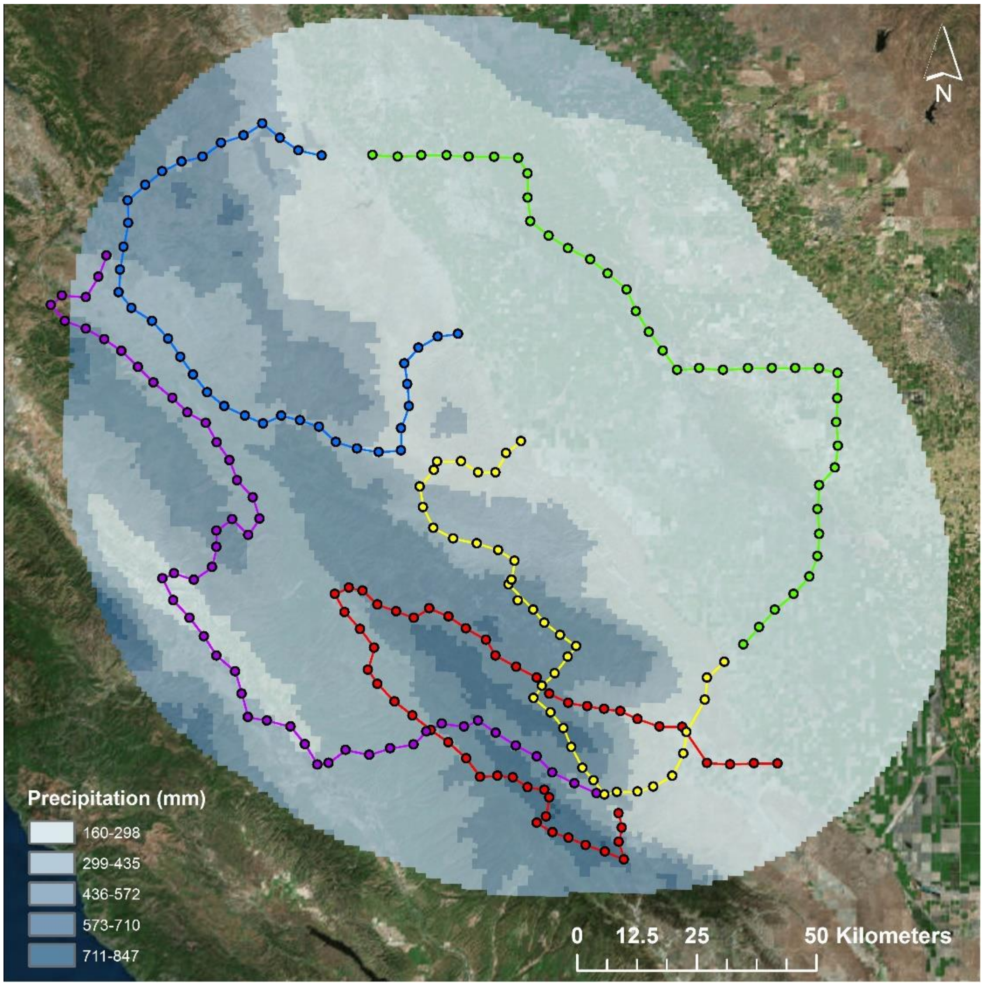

Figure 3. Driving survey routes for California ground squirrel (*Otospermophilus beecheyi)* within a 50km buffer of the Ciervo-Panoche Natural Area. Each line is a survey route and each point is a survey stop. Blue colors represent different routes, driven on different days. Average annual precipitation is displayed in 5 numerical categories approximately 130mm each, darker blue areas are the lowest precipitation values.

## Species Distribution Modeling

I used Maxent to create species distribution models for *D. ingens* and *O. beecheyi* (Phillips et al. 2006). Maxent is a machine learning algorithm that calculates the maximum entropy probability distribution of occurrence points under a set of environmental constraints. Maxent samples background locations (default = 10,000) to compare to presence locations. No inference is made as to whether background locations are presence or absence sites, hence they are considered "available". With the large number of background points sampled, there is a near certainty that they include both presence and absence locations. Once a model is estimated, Maxent projects it to the entire study area, resulting in a map of values ranging from zero to one. For the purposes of this study, Maxent values are referred to as habitat suitability. Bean et al. (2014b) found that Maxent accurately predicts habitat suitability for *D. ingens* at a coarse scale, but is less accurate in estimating fine-scale habitat quality which incorporates population vital rates. I first created a suite of models of current *D. ingens* distribution and then included future projections for temperature and precipitation, according to the Community Climate System Model's emissions scenario under the most severe representative concentration pathway (rcp85) (Gent et al. 2011).

For current climatic conditions, I created species distribution models for three different subsets of the *D. ingens* range: one for the Panoche, one for the Carrizo, and a third, rangewide model that contains both populations. After selecting biologically relevant predictor variables (Table 1), I ran a Pearson's correlation test to avoid pairing variables that were strongly correlated. I assumed that a correlation value above 0.6 indicated a strong relationship and decoupled those variables so that both remained potential variables, but were not included in the same models (Pearson 1920). Using a jackknife test of variable importance, performed by Maxent, and each variable's percent contribution to the models, I finalized the set of variables available for candidate models. Although aspect was considered for initial candidate selection, after running preliminary models, it was removed from the final candidate model set for lack of contribution. I adjusted the beta value, a regularization parameter designed to optimize data fitting, on the preliminary models ($\beta = 0.5$, 1, and 2) and used Akaike's Information Criterion corrected for small sample size (AICc) to assess model fit. The top models were all created using $\beta = 1$, thus I determined that this value was the most appropriate (Morales 2017). I used the default auto-features setting to select feature types and selected the complementary log-log output for Maxent predictions, constraining the output values between zero and one. With these constraints, I constructed a final candidate model set of 43 different combinations of the seven variables for model selection (Appendix A).

The best model for each geographic subset was chosen using AICc and model discrimination ability was assessed using area under the curve (AUC). The top model from each extent was iterated four times, with a 25% subset of presence locations. I calculated the coefficient of variation of the Maxent outputs (habitat suitability) of the four runs. Additionally, I calculated the Continuous Boyce Index (CBI), which measures model accuracy using background points, and does not require true absences (Hirzel et al. 2006). CBI is an improvement of the Boyce Index that uses a moving window rather than discrete bins to estimate the Spearman rank correlation of the ratio of predicted to expected presence locations (Boyce et al. 2002). The moving window overcomes the Boyce Index's sensitivity to the number of discrete bins of suitability. I calculated CBI using ten bins with a moving window between the maximum and minimum suitability values. I used 75% of the data to train the model and 25% to test using CBI. The result is a value between negative one and one, where a positive one represents a model that accurately predicted presence, zero means the model is no better than random chance, and negative values predict presence in the areas of the lowest suitability (Hirzel et al. 2006). I also estimated CBI by projecting each population's model to the other population's geographic extent, which provides an independent test of each population's model.

Due to habitat loss, a contemporary model may not capture the full range of the environmental niche. Rutrough et al. (In prep) built a historical *D. ingens* distribution model based on pre-1950 aerial imagery containing burrow mounds. Using predictions of climate under a high-emissions scenario, I projected the model of historical distribution into the future. Then, based on habitat suitability, compared the predicted range contraction from my models to that of the historical model. An estimate of historical niche breadth should be broader than the contemporary model. The historical model includes areas that are no longer occupied, mostly due to agricultural expansion, and could take in to account combinations of environmental factors absent in the current range.

The current and future modeling process was then repeated with *O. beecheyi* occurrence data to create a similar suite of distribution models. The models included presence locations from anecdotal sightings, driving surveys, and GBIF, an open access resource for biodiversity data (Global Biodiversity Information Facility, GBIF Secretariat 2017).  I modeled three geographic extents, slightly different from the *D. ingens* models: California-wide—rather than rangewide—and locally within the Panoche and Carrizo. I used only GBIF locations to create the California-wide models, to avoid biasing my study areas with increased point locations. For the Panoche and Carrizo models I included survey locations and anecdotal sightings, but thinned the locations using the geogThin function in the R package enmSdm so that clusters of squirrels within one pixel (pixel width = 900m) were represented by a single location (Muscarella et al. 2014, Smith 2018).

To visualize contemporary and future distributions and inform management, I selected threshold values to convert my continuous habitat suitability models to maps excluding the lowest suitability values. For all extents, the threshold for “not suitable” was selected based on the 5th percentile suitability value of all occurrence points within the respective current model. Thus, values where 95% of presence points occur were considered suitable and the lower 5% were considered “not suitable”. I subdivided suitability into two categories, low and high. I considered “low” suitability to be between the 5th and 50th percentile, and all greater values were considered “high” suitability. I used the same values for thresholding future models. These threshold values were only use for mapping purposes; unthresholded models were used for further analyses.

## Niche Overlap

Maps of the three top *D. ingens* models (Panoche, Carrizo, rangewide) were compared to evaluate niche overlap and the evidence for separate adaptation in the Panoche and Carrizo populations. Subsequently, the same models were projected into the future using predicted climate variables according to the emissions scenario, and future overlap was calculated. Low niche overlap would indicate that populations experience different environmental regimes, and could suggest adaptation in a specialist species. I used Warrens I (Warren et al. 2008) to calculate the degree of niche overlap. This similarity statistic ranges from zero to one with a value of one indicating identical niche models.

Warren's *I* is calculated as follows,

$$I(p_X, p_Y) = 1 - \frac{1}{2} H(p_x, p_y)$$

where $p_x$, and $p_y$ are probability distributions of the models under comparison and *H* is Hellinger Distance (van der Vaart 1998, Warren et al. 2008):

$$H(p_X, p_Y) = \sqrt{\sum_i (\sqrt{p_{X,i}} - \sqrt{p_{Y,i}})^2}$$

where *i* is a cell in the raster of habitat suitability. These calculations were conducted using the ENMeval package in R (Muscarella et al. 2014). High overlap between populations would indicate that they experience range limitations from similar environmental variables. Changes in future overlap reveal whether populations are likely to have similar limitations or will potentially experience different future constraints.

The habitat suitability maps of both *D. ingens* and *O. beecheyi* were then compared to observe niche overlap. This allowed for a comparison of the current overlap between species and a prediction of future overlap, indicating whether competition is likely to become an issue.

# RESULTS

## Data Collection

### Live Trapping

Across the range, pooling all years, there were 439 total sites surveyed for *D. ingens*. In total 301 of these sites resulted in a positive detection; 197 presence locations were in the Panoche population, 101 in the Carrizo, and three in the range between populations. At these 301 sites 1,583 individuals were uniquely identified.

### Driving Surveys

Driving surveys for *O. beecheyi* resulted in 228 thinned locations overall, 165 in the Panoche and 34 in the Carrizo.

## Species Distribution Modeling

### *D. ingens*

A different model was created for the Carrizo and Panoche populations as well as the rangewide extent, with candidate models including various combinations of three to five of the seven variables. The top models for all three geographic extents were unambiguous; all other models had ΔAICc greater than seven. The Panoche model included climatic water deficit, minimum temperature, maximum temperature, percent clay, and slope (Table 2, Figure 4). The Carrizo model included precipitation, maximum temperature, percent clay and slope (Table 2, Figure 4). The rangewide model included precipitation, minimum temperature, maximum temperature, clay, and slope (Table 2, Figure 5). The general trends present across all extents include a high preference for low slope, and a peak in suitability around 23% clay in the soil. All extents included maximum temperature as a variable, but while the Panoche and rangewide models show high suitability at high maximum temperatures, the Carrizo model showed a negative relationship with maximum temperature. The Panoche and rangewide models showed a peak in suitability at around 9°C for minimum temperature. The Carrizo and rangewide models showed a sharp peak in suitability at 210 mm of mean annual precipitation. Climatic water deficit was only included in the model for the Panoche and peaked in suitability around 1080 mm (Appendix B). All top models had AUC scores above 0.9 (Appendix C). The CBI values were also all above 0.85, which indicates that the models accurately predicted suitability. Figures reflect suitability values in which 95% of detections occurred (5th percentile threshold).

Table 2. Inclusion of variables in the top Maxent models for four different study extents, the Ciervo-Panoche Natural Area, the Carrizo Plain National Monument, and rangewide for giant kangaroo rats (*Dipodomys ingens*) and California-wide for California ground squirrels (*Otospermophilus beecheyi*). White rows correspond to *D. ingens* and grey bars are *O. beecheyi*. A blank cell indicates that a variable was not included, while the values represent the percent contribution of that variable to the model. The variables from left to right are as follows: mean annual precipitation, mean annual climatic water deficit, mean annual minimum temperature, mean maximum annual temperature, mean percent sand in soil, mean percent clay in soil, and degrees of slope.

| | **Precip** | **CWD** | **Min Temp** | **Max Temp** | **Sand** | **Clay** | **Slope** |
|---|---|---|---|---|---|---|---|
| **Panoche** | | **31** | **13** | **16** | | **7** | **33** |
| **Carrizo** | **57** | | | **4** | | **18** | **21** |
| **Rangewide** | **38** | | **11** | **9** | | **20** | **22** |
| **Panoche** | | **35** | | **9** | **51** | | **5** |
| **Carrizo** | | **30** | | **3** | | **9** | **58** |
| **California** | **65** | | **17** | | | | **18** |

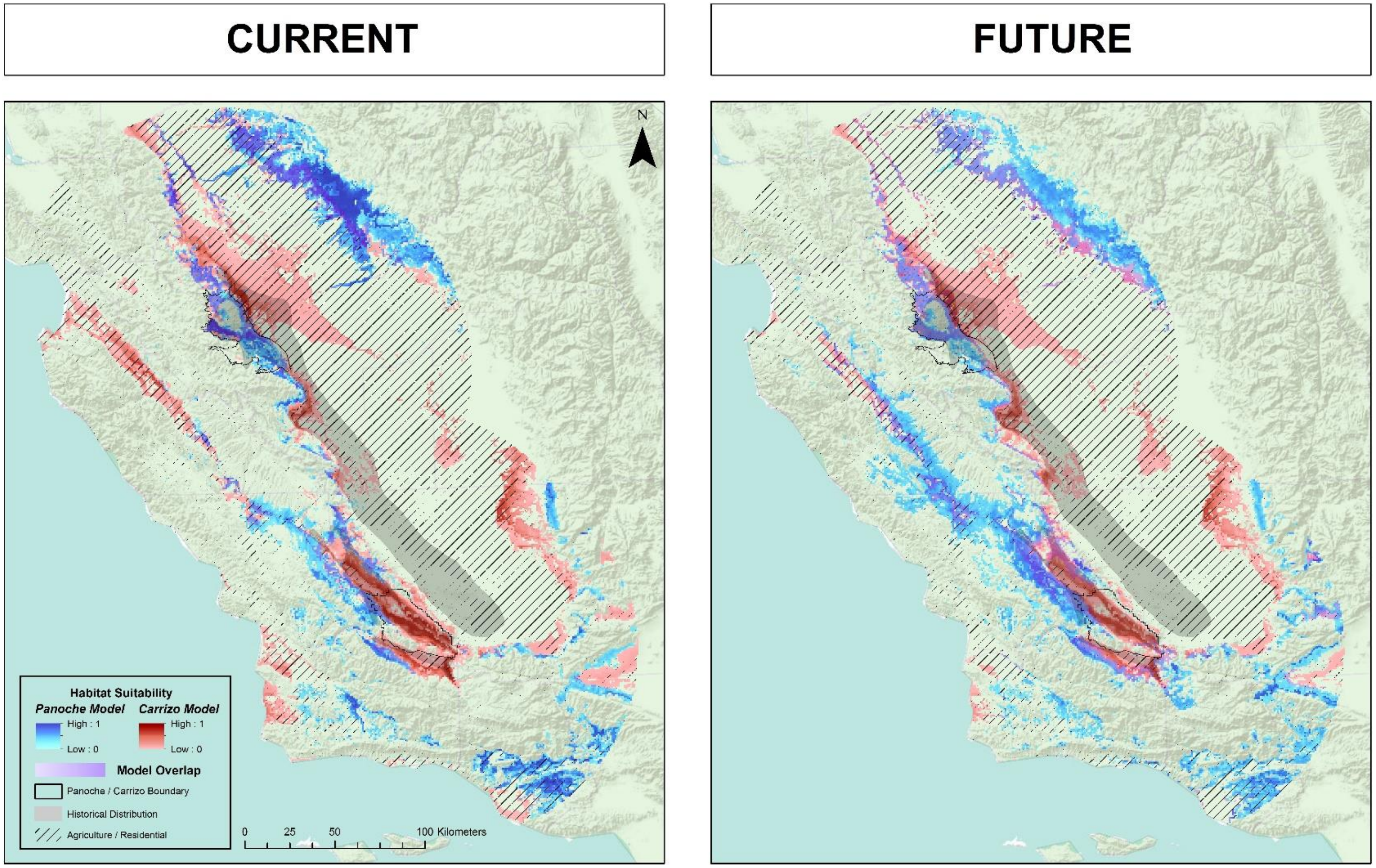

Figure 4. Current (1980-2010) and future (2070-2099) species distribution models for giant kangaroo rats (*Dipodomys ingens*). Models were trained locally and projected rangewide. Higher suitability is indicated by dark shading. The model trained in the Panoche is shown in blue and the model trained in the Carrizo is shown in red. Purple areas indicate overlap between the two models. The gray shading indicates the historical distribution presented by Williams et al. (1992) and the crosshatching shows areas of agriculture or residential use. The future map (right) was projected using CCSM4 rcp8.5

When populations were modeled together in the rangewide model, the prediction of future habitat suitability was low and covered a small area (Figure 5). However, when the two populations were modeled separately and each projected into the future (2070-2099), less range contraction was predicted (Figure 4). The future projection of the historical model also predicts less range contraction than the rangewide model (Figure 6).

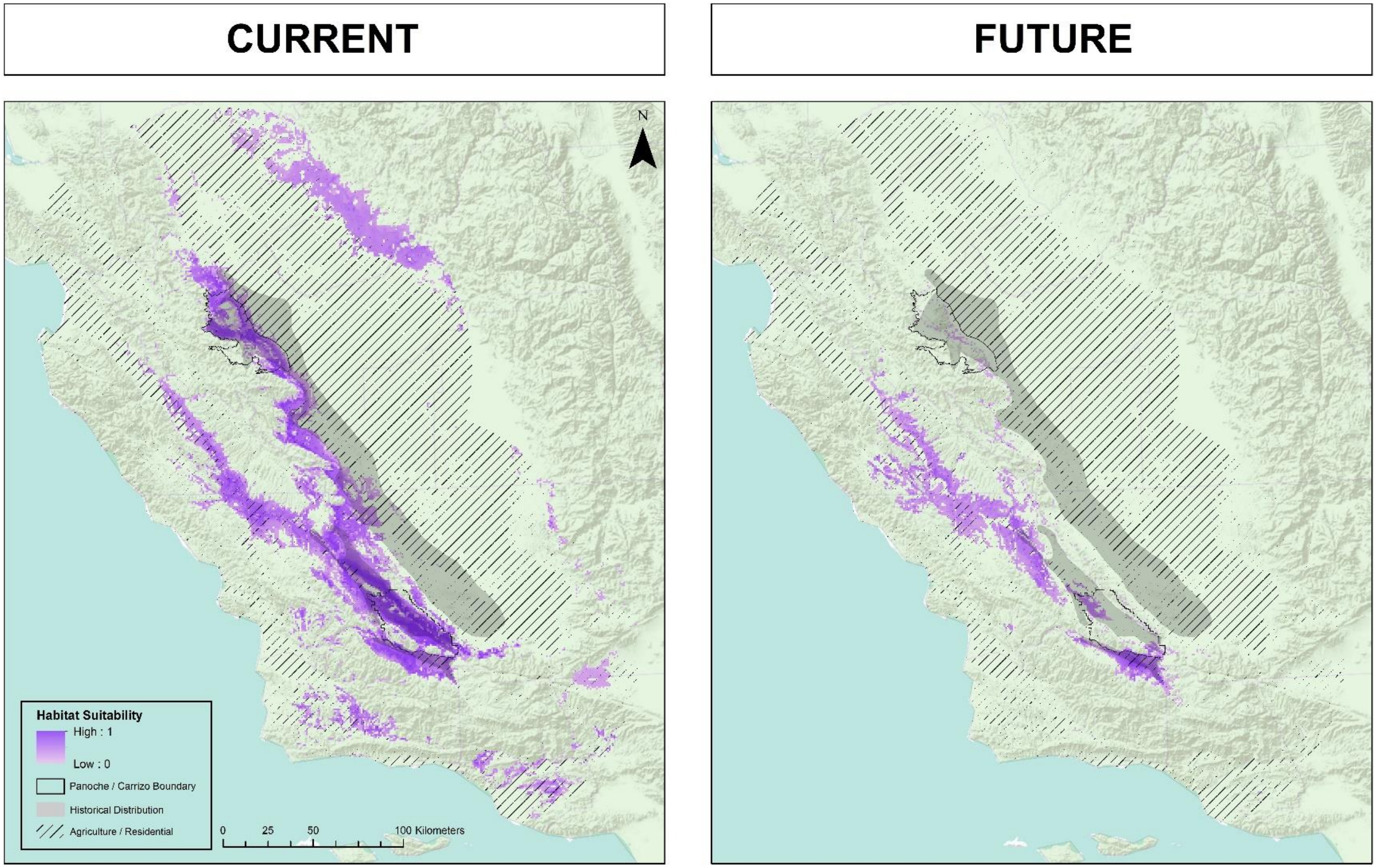

Figure 5. Current (1980-2010) and future (2070-2099) species distribution models for giant kangaroo rats (*Dipodomys ingens*). Models were trained rangewide including all presence locations. Higher suitability is indicated by darker shading. The gray shading indicates the historical distribution presented by Williams et al. (1992) and the crosshatching shows areas of agriculture or residential use. The future map (right) was projected using CCSM4 rcp8.5

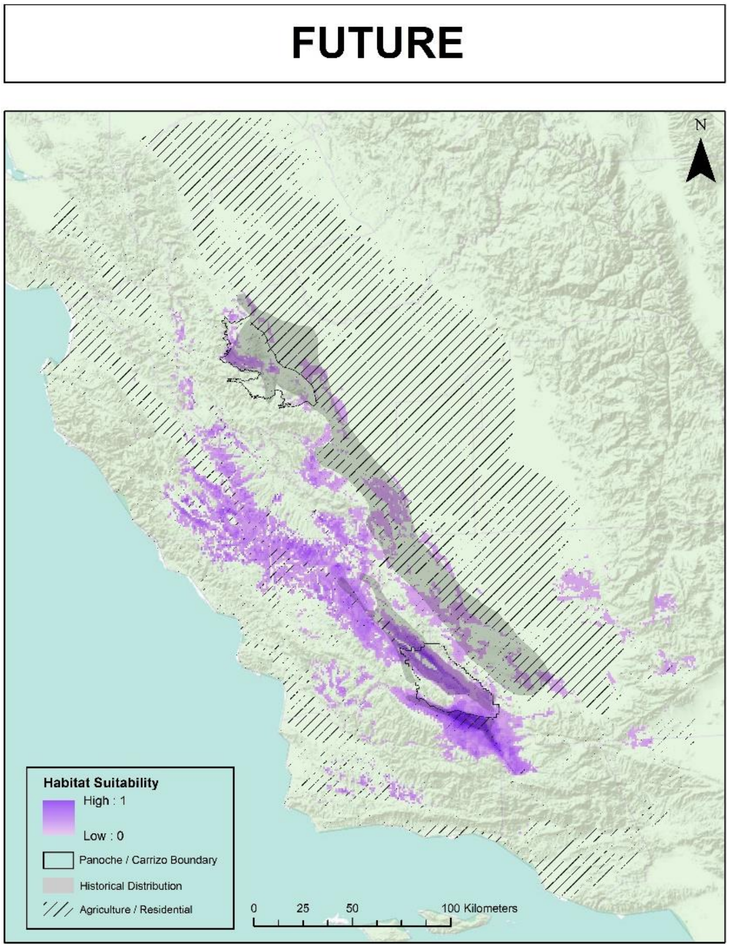

Figure 6. Future (2070-2099) species distribution model for giant kangaroo rats (*Dipodomys ingens*), based on their historical distribution. Rutrough at al. created a distribution model from rangewide historical aerial imagery (unpublished data). Here, the same model is projected into 2070-2099 using CCSM4 rcp8.5. The gray shading indicates the historical distribution presented by Williams et al. (1992) and the crosshatching shows areas of agriculture or residential use.

### *O. beecheyi*

The top models for all three extents — Panoche, Carrizo, and California-wide — differed but were unambiguous (Table 2, Figure 7). Habitat suitability for all extents included a strong effect of low slope. Habitat suitability in the Panoche showed a positive relationship with the percent of sand in the soil. Similarly, Carrizo showed a negative relationship with the percent of clay. Maximum temperature peaked in suitability in both population-level models at about 26°C. The California-wide model peaked in suitability at 6°C minimum temperature and 190 mm precipitation. Climate water deficit in both the Panoche and Carrizo caused a peak in suitability at between 1000-1200 mm (Appendix D). All models had AUC values above 0.8 (Appendix C) and CBI values for the Panoche and California were 0.99 and 0.91 respectively, while the CBI for the Carrizo was 0.79.

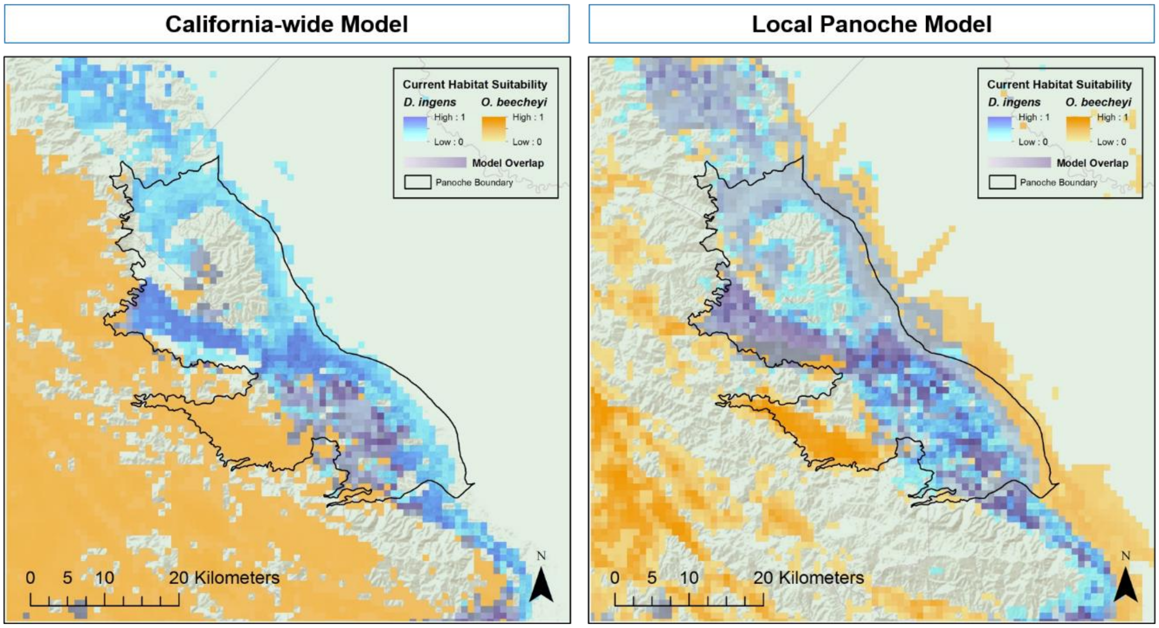

Figure 7. Current (1980-2010) species distribution models for California ground squirrels (*Otospermophilus beecheyi*) and giant kangaroo rats (*Dipodomys ingens*). All maps include a *D. ingens* model trained locally in the Panoche (blue). On the left, the *O. beecheyi* model was trained across California and on the left was locally trained in the Panoche (orange). Higher suitability is indicated by dark shading. Purple areas indicate overlap between the two species' models.

## Niche Overlap

All *D. ingens* models were positively correlated, except the relationship between the Panoche and Carrizo models, which was near zero, but slightly negative. When calculating CBI to compare the Panoche model's ability to predict suitability in the Carrizo, and vice versa, the values were well below zero, at about -0.8, indicating these models predicted the highest suitability in the least suitable areas. Niche overlap between the current Panoche and Carrizo populations was moderate (Warren's $I = 0.43$). Niche overlap between *O. beecheyi* and *D. ingens* in the Panoche was higher than overlap between species in the Carrizo (Figure 8). Although the models of niche are consistent from current to future, the geographic availability of combinations of environmental factors changes, this allows for different levels of niche overlap in the future. Niche overlap decreased between *D. ingens* populations in the future ($I$ = 0.43 to 0.35). Niche overlap between the Carrizo population and *O. beecheyi* also decreased ($I$ = 0.52 to 0.46), however, overlap between the Panoche population and *O. beecheyi* increased in the future ($I$ = 0.63 to 0.74) (Figure 8)

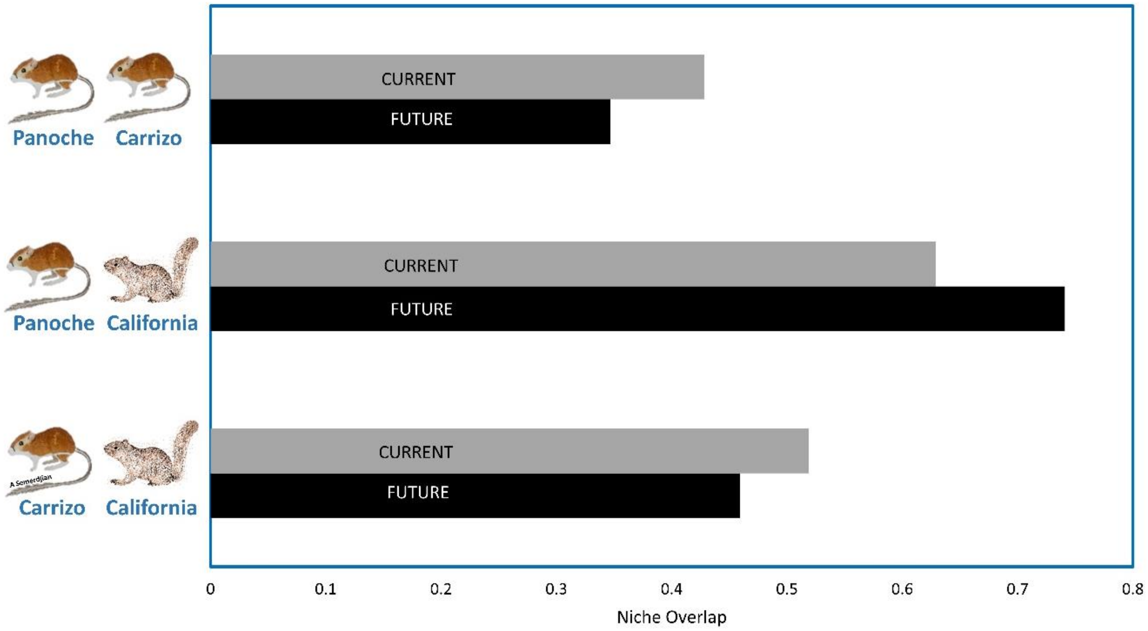

Figure 8. Values of niche overlap between local habitat suitability models for giant kangaroo rats (*Dipodomys ingens*) in the Ciervo-Panoche Natural Area and Carrizo Plain National Monument, as well as between local *D. ingens* models and California ground squirrel *(Otospermophilus beecheyi*) across California. Grey bars indicate current niche overlap according to Warren's I and black bars are predicted future overlap in 2070-2099.

# DISCUSSION

## Species Distribution Modeling

Species distribution models of *D. ingens* in the past have focused on rangewide or Carrizo-specific models, leaving the Panoche population relatively underrepresented (Bean et al. 2014a). Habitat destruction and climate change have contributed to range contraction, isolation, and potentially local adaptation. My comparison of *D. ingens* local and rangewide models revealed niche differences between populations, providing evidence that the two populations should be treated separately. Rutrough et al. (In prep) created a historical distribution model which I projected according to current climatic conditions. Using the historical model to predict current habitat suitability, the Carrizo was predicted to remain relatively stable, but the Panoche was predicted to decrease in suitability. Hence, the persistence of *D. ingens* in the Panoche is an indicator of adaptation through time and supports the increased local accuracy of population-specific models.

A review of range shifts in response to climate change revealed that observing species as a whole masks inconsistencies between populations (Gibson-Reinemer and Rahel 2015). Tracking the shifts of populations in different geographic areas showed idiosyncratic responses to changing climate. In fact, 50% of species studied shifted in different cardinal directions. My study of *D. ingens* populations provides more evidence for not generalizing range shifts for entire species as a unit, but considering population differences across the range. In contrast, population-specific models may more accurately predict future distributions and identify range limiting factors in different geographic areas.

For *D. ingens,* the environmental factors included in the top local models were similar for both populations, with the exception of the precipitation variable. Previous distribution modeling and habitat associations for this species showed similar environmentally suitable variables, such as low slope and hot temperatures, and have highlighted the importance of precipitation (Grinnell 1932, Williams 1992, Bean et al. 2014a). The limitation imposed by precipitation could be defined by either excessive or insufficient rainfall. In the Carrizo model, precipitation was an influential variable, contributing 58% to the model (Table 2). Excessive precipitation may cause direct effects of water infiltration and burrow collapse (Germano et al. 2001). Alternatively, precipitation could better define the areas limited by too little water, hindering primary productivity.

The Panoche model included climatic water deficit rather than mean annual precipitation. This is consistent with the Vegetation Hypothesis, suggesting *D. ingens* in the Panoche are more limited by consequences of dense vegetation due to increased water availability than they are by direct effects of precipitation. This population's mechanism to reduce the impact of precipitation likely occurs underground, such as selection for sturdier soils, or constructing more complex or longer burrow systems to shelter food caches. However, increased precipitation produces more dense, non-native vegetation, providing the next adaptive challenge to persistence. Semerdjian et al. (In prep) have shown that the Panoche population has lower average body weight compared to the Carrizo population, facilitating navigation through thick grasses, but potentially increasing the risk of competition from similarly sized species, like Heermann's kangaroo rat (*D. heermanni*, Figure 9).

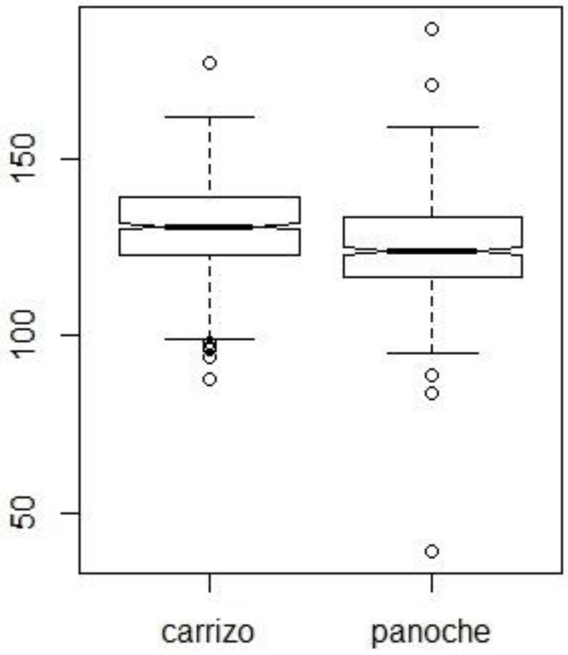

Figure 9. A notched boxplot of giant kangaroo rat (*Dipodomys ingens*) weights (g) from two poulations, the Carrizo Plain National Monument (left) and the Ciervo-Panoche Natural Area (right). Weight is significantly lower in the Panoche population. Reflects data from Semerdjian et al. In prep. which includes the same individuals analyzed in this text.

## Future Predictions

The local models predicted far less range contraction than the rangewide model. The local models also predict less contraction than the historical model which modeled the species as a whole (Rutrough et al. In prep). Treating the populations separately allows for the consideration of respective local adaptations when projecting into the future, thus identifying areas where either population could survive, rather than the overlap between them (Figure 4).

## Niche Overlap

Moderate niche overlap between populations indicates some niche divergence. The local models indicate retention of some niche characteristics shared between populations, namely a strong association with low slope, but emphasize the developed variation between them, such as an association with lower maximum temperatures in the Carrizo, and the importance of climatic water deficit over precipitation in the Panoche. While both populations share some fundamental environmental associations, the differences in climatic factors could alter their response to environmental change and disparate reactions to species interactions.

The potential for competition was approximated using niche overlap between species. The results presented were estimated from the California-wide niche of *O. beecheyi,* which captures much of the range of the environmental associations of this generalist species. While this comparison suggested that niche overlap was greatest in the Panoche population, local models highlight the potential for interaction on a finer scale.

The niche overlap between local species models was similar between the two populations, indicating that both *D. ingens* populations have the same potential for interspecific competition at this scale. However, the habitat suitability value of the geographic areas of niche overlap is important to consider. In the Carrizo, overlap occurs in peripheral areas that are currently considered inaccessible to *D. ingens* due to dispersal limitations or land use. In contrast, the areas of overlap in the Panoche are within confirmed current *D. ingens* habitat, including areas where the two species have been observed in close proximity. Here I focus on the Panoche local model because the Carrizo model has a very small sample size because it was not surveyed systematically (Figure 7).

Overall, the niche overlap between species in the Panoche was greater and included more critical areas. In particular, the Panoche Valley is an area of high suitability for *D. ingens* with confirmed occupancy, but it is at high risk from solar development and *O. beecheyi* habitation (USFWS 2010). Both species have been observed in the area, but spatial partitioning generally prevents them from occupying the same sites. The dynamics of interactions between the two species within the same site have yet to be defined, but based on my findings, such interactions warrant future study.

### Future Predictions

I found that the degree of niche overlap between species and populations changes in the future. Although the prediction of habitat suitability across the landscape varies in the future, the model that is projected remains the same. Accordingly, niche overlap may be expected to remain stable. However, Warren’s I is calculated from a geographical prediction of the models, meaning that the calculation is inherently spatial. The probability distributions are compared, which means the extent of the study area and the availability of combinations of environmental predictors affect the amount of overlap.

Since overlap was predicted to decrease between future populations, management should focus on protecting locally suitable areas. Hence, treating populations similar to those in a sub-species management plan would be warranted. Protection of areas of overlap is important, but if the populations' niches drift farther apart, the individually suitable areas will become more important.

Niche overlap is also predicted to increase between *D. ingens* and *O. beecheyi* in the future. This combined with continued land conversion for human development may contribute to novel competition. An increase in geographic and niche overlap with *O. beecheyi* could negatively affect the dominance of *D. ingens* and increase the impact of biotic interactions on range limitation of *D. ingens*.

## Limitations and Future Directions

While the species distribution models in this study attempt to estimate the current niche and use it to forecast the future range, there are limitations in the models themselves as well as the niche being defined. Because so much of the historical range of *D. ingens* has been converted for anthropogenic use, estimating the fundamental niche using contemporary presence records may be impossible. Modeling the contemporary distribution likely represents the current realized niche for both populations, thus the future predictions assume the restrictions placed on the populations will persist and relationships to environmental variables will be maintained.

The future predictions of habitat suitability are likely optimistic because they do not consider the importance of land use or vegetation type. Agriculture and other anthropogenic development prevent *D. ingens* occupation, affecting the amount of habitat available to them (USFWS 1998). My models estimate that 27% of currently suitable habitat is already in use as agriculture. However, due to a lack of data and ability to predict future land use, it was omitted from the modeling process, despite its inherent importance.

On the other hand, since agriculture is included as “available” to *D. ingens* in the models but there are no positive detections in those areas, environmental suitability of regions of current agriculture may be underestimated. This could be important when restoring areas of human development into viable habitat. Although, even with encouragement and compensation to fallow agricultural land, without knowledge of the timeline or ability of recolonization, we cannot include it in predictive modeling. For management purposes, we must consider these areas to be outside the scope of *D. ingens* range until restoration occurs and recolonization is documented. An ongoing project by The Nature Conservancy seeks to identify suitable areas for fallowing and restoration, hopefully providing valuable data to inform further modeling. Additionally, vegetative communities can alter habitat suitability, whether relating to food resources or locomotion, but without future knowledge of vegetation changes, this variable cannot be incorporated into the models.

Furthermore, novel competitors could limit range shifts or expansion. Most current models attempt to capture competition through associations with abiotic proxies. This most likely means including environmental or demographic variables important to the distribution of the competitor in the models for the target species (Leathwick and Austin 2001). For example, canopy cover may not be important to the target species, but may reliably define the distribution of a competitor, thus including canopy cover in the model may account for the separation in distribution between species. The alternative approach, used here, is to model the target species distribution independently and constrain it by the competitor's distribution (Guisan and Thuiller 2005). In the future, even if agricultural land is restored, of the cultivated areas otherwise suitable for *D. ingens,* 33% is also suitable for *O. beecheyi*. However, future efforts could model *O. beecheyi* removal experiments to estimate the potential effects on *D. ingens* if agricultural land is recovered.

While I did not directly model the effect of *O. beecheyi* in the future range predictions, niche overlap is expected to increase in the Panoche, creating more potential for competition. In the future, it would benefit range prediction and management to incorporate potential antagonistic interactions into *D. ingens* distribution models. Community ecologists are in pursuit of an effective method of modeling species co-occurrences in this manner. Frameworks have been developed for joint species distribution models, but while their use is gaining popularity, it is a recent development mostly adapted for generalized additive or generalized linear models (Pollock et al. 2014, Cazelles et al. 2016).

In the future, incorporation of these key elements would create a more accurate model, improving the predictions of future ranges. This may mean multi-species distribution modeling to directly incorporate effects of biotic interactions. This method could also be used to include the effects of vegetation by creating future models of food sources or inhibitory vegetation. The colonization of fallowed farmland may prove important in range expansion; this possibility should be investigated to be included in future modeling.

# MANAGEMENT IMPLICATIONS

The current recovery plan for *D. ingens* highlights the importance of acquiring and conserving specific locations of confirmed occupancy (Williams et al. 1998). An updated management plan for *D. ingens* should consider local adaptation, biotic interactions, and historical, current, and future habitat suitability. Protecting areas of high habitat suitability from development is essential for the survival of this keystone species. Suitable areas of overlap between the historical, local, and rangewide models should be of particular concern and importance, but of these three potential futures, the overlap between historical and local models should be a priority (Figure 10). This combination retains historical niche characteristics while incorporating the effects of local adaptation over time. Within the priority areas, those occupied by *O. beecheyi* populations should be considered less than ideal habitat.

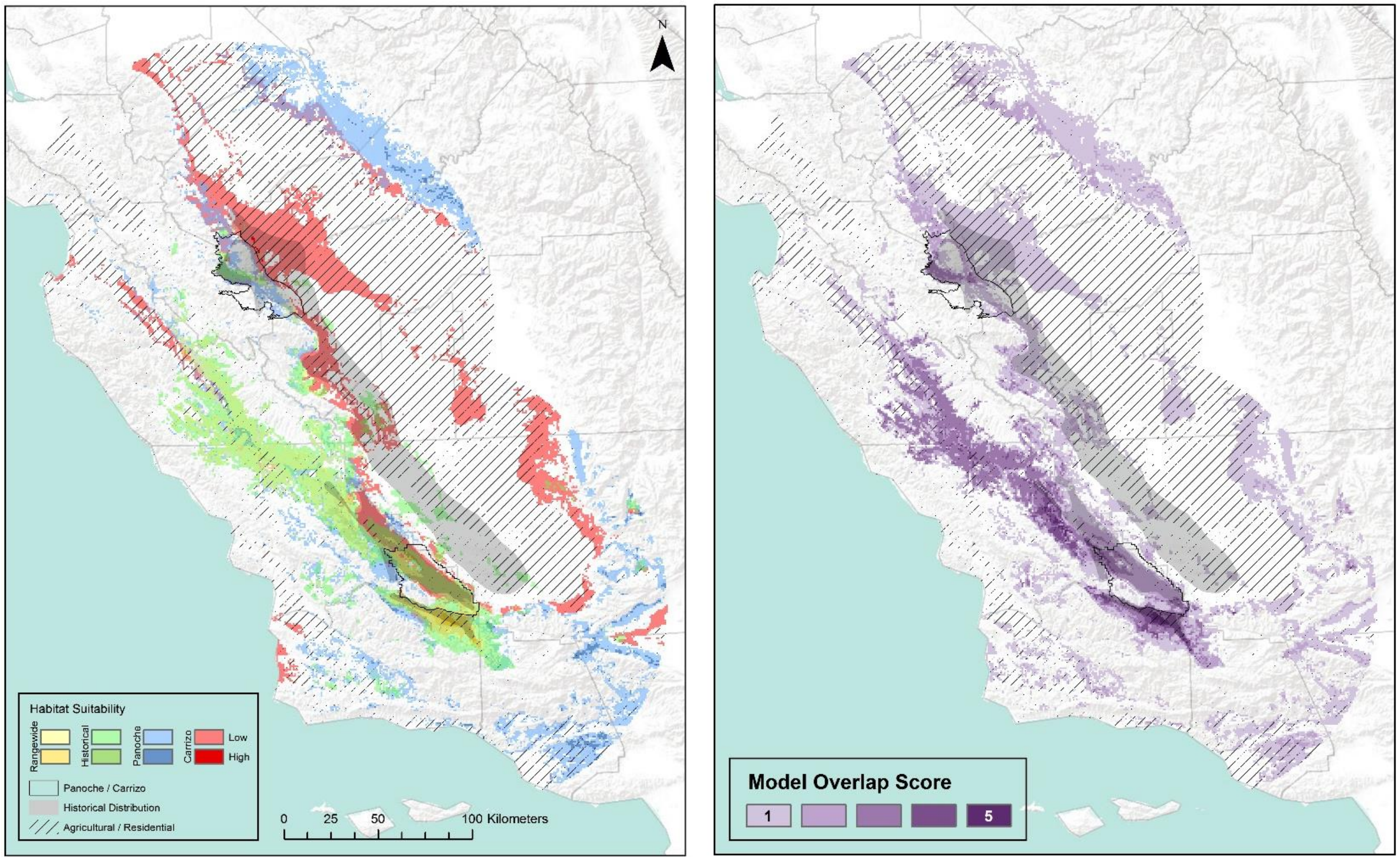

Figure 10. Left: Four separate future projections of giant kangaroo rat (*Dipodomys ingens*) habitat suitability. Blue and red are models trained locally, within the Panoche and Carrizo populations, respectively. The green model was trained rangewide, including both populations. The yellow is the historical distribution based on aerial imagery (Rutrough et al. In prep). Right: The four models on the right combined. Low suitability was assigned a score of one, high suitability a score of two and the models were all added. Darker shading indicated higher suitability and more model agreement. All models are projected into 2070-2099 using CCSM4 rcp8.5. The gray shading indicates the historical distribution presented by Williams et al. (1992) and the crosshatching shows areas of agriculture or residential use.

Of particular interest is Cuyama Valley, just south of the Carrizo. Future suitability in the Cuyama Valley is high according to the historical, rangewide, and local models (Figure 11). The valley is currently used for ranching, agriculture and oil production, but is predicted to be suitable for both populations in the future. Another important location is the Panoche Valley on the western edge of the Panoche (Figure 11). This area is threatened by solar development, but remains one of the most suitable areas for both populations, including the projections from the historical model. While these areas are within the current range or directly adjacent, the models identify suitable areas at mostly mid-range latitudes further east of the current range, in the San Juan Creek area. *D. ingens* has a relatively short dispersal distance (~2.5km, Alexander 2016), but fortunately already inhabits the southern end of this suitable area, potentially allowing them to colonize areas further north that are anticipated to become or remain suitable in the future. Areas predicted to increase in suitability that are not already occupied or within dispersal distance may pose a challenge to colonization. Previous attempts at translocation of *Dipodomys spp*. (*D. ingens, D. heermanni, D. nitratoides*) have failed to establish colonies, resulting in the death of the founding members and the crash of populations (Germano 2010, Williams et al. 1993).

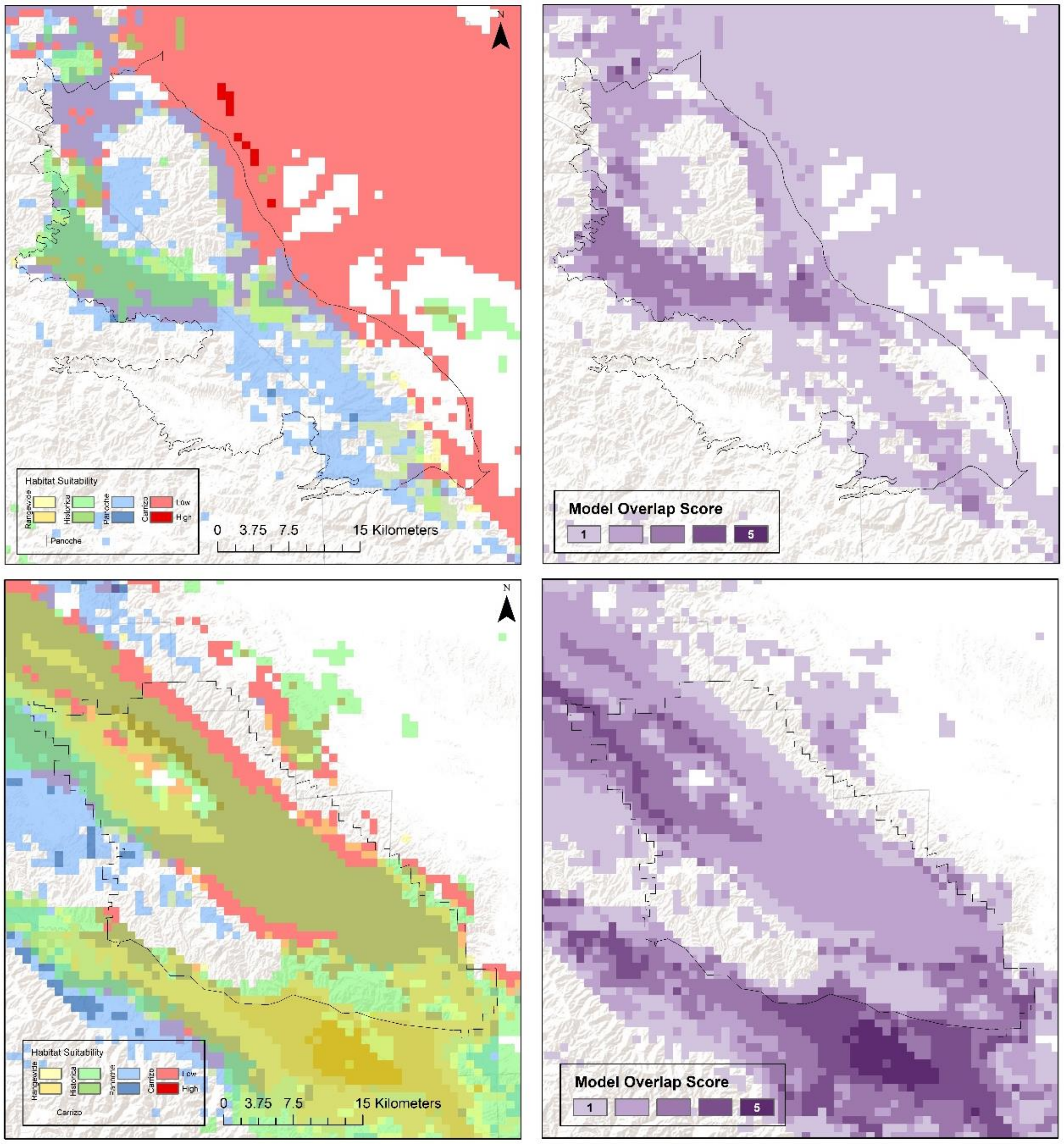

Figure 11. Left column: Four separate future projections of giant kangaroo rat (*Dipodomys ingens*) habitat suitability. Blue and red are models trained locally, within the Panoche and Carrizo populations, respectively. The green model was trained rangewide, including both populations. The yellow is the historical distribution based on aerial imagery (Rutrough et al. In prep). Right column: The four models on the right combined. Low suitability was assigned a score of one, high suitability a score of two and the models were all added. Darker shading indicated higher suitability and more model agreement. All models are projected into 2070-2099 using CCSM4 rcp8.5.

Conservation prioritization based on future suitability would improve the chance of survival for *D. ingens* populations. This may include a combination of future distribution predictions, connectivity modeling (i.e. Alexander 2016), and strategic land conservation. The protection of this keystone species and ecosystem engineer will help maintain the landscape for other taxa, and help ensure the health of the community in the future.

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# APPENDIX A

Appendix A. Candidate Maxent model set for giant kangaroo rats (*Dipodomys ingens*) and California ground squirrel (*Otospermophilus beecheyi*) and the ΔAICc values (only comparable within columns). Variables include mean annual precipitation (mm), mean annual climatic water deficit (mm), mean annual minimum temperature (°C), mean annual maximum temperature (°C), percent sand in soil, percent clay in soil, and degree of slope. Grey shading in the leftmost column indicates that model was a top model in one of the six scenarios (columns). Grey shading in the remaining columns highlight the ΔAICc scores of the top ten models for that spatial extent.

| **Spatial Extent**<br>**Model Variables** | **Panoche**<br>*D. ingens* | **Carrizo**<br>*D. ingens* | **Rangewide**<br>*D. ingens* | **Panoche**<br>*O. beecheyi* | **Carrizo**<br>*O. beecheyi* | **California**<br>*O. beecheyi* |
|---|---|---|---|---|---|---|
| cwd, mintemp, maxtemp, clay, slope | 0 | 24 | 140 | 130 | 2036 | 832 |
| cwd, mintemp, maxtemp, sand, slope | 42 | 52 | 139 | 79 | 2459 | 813 |
| precip, mintemp, maxtemp, clay, slope | 66 | 14 | 0 | 69 | 2168 | 405 |
| precip, mintemp, maxtemp, sand, slope | 133 | 79 | 44 | 17 | 2137 | 394 |
| mintemp, maxtemp, clay, slope | 98 | 96 | 435 | 220 | 2632 | 829 |
| mintemp, maxtemp, sand, slope | 147 | 119 | 452 | 158 | 3017 | 1289 |
| cwd, maxtemp, clay, slope | 135 | 52 | 241 | 258 | 0 | 693 |
| cwd, maxtemp, sand, slope | 168 | 54 | 209 | 209 | 2463 | 706 |
| cwd, mintemp, clay, slope | 90 | 23 | 193 | 139 | 1867 | 668 |
| cwd, mintemp, sand, slope | 171 | 47 | 186 | 87 | 2610 | 627 |
| cwd, mintemp, maxtemp, slope | 110 | 42 | 251 | 287 | 1686 | 727 |

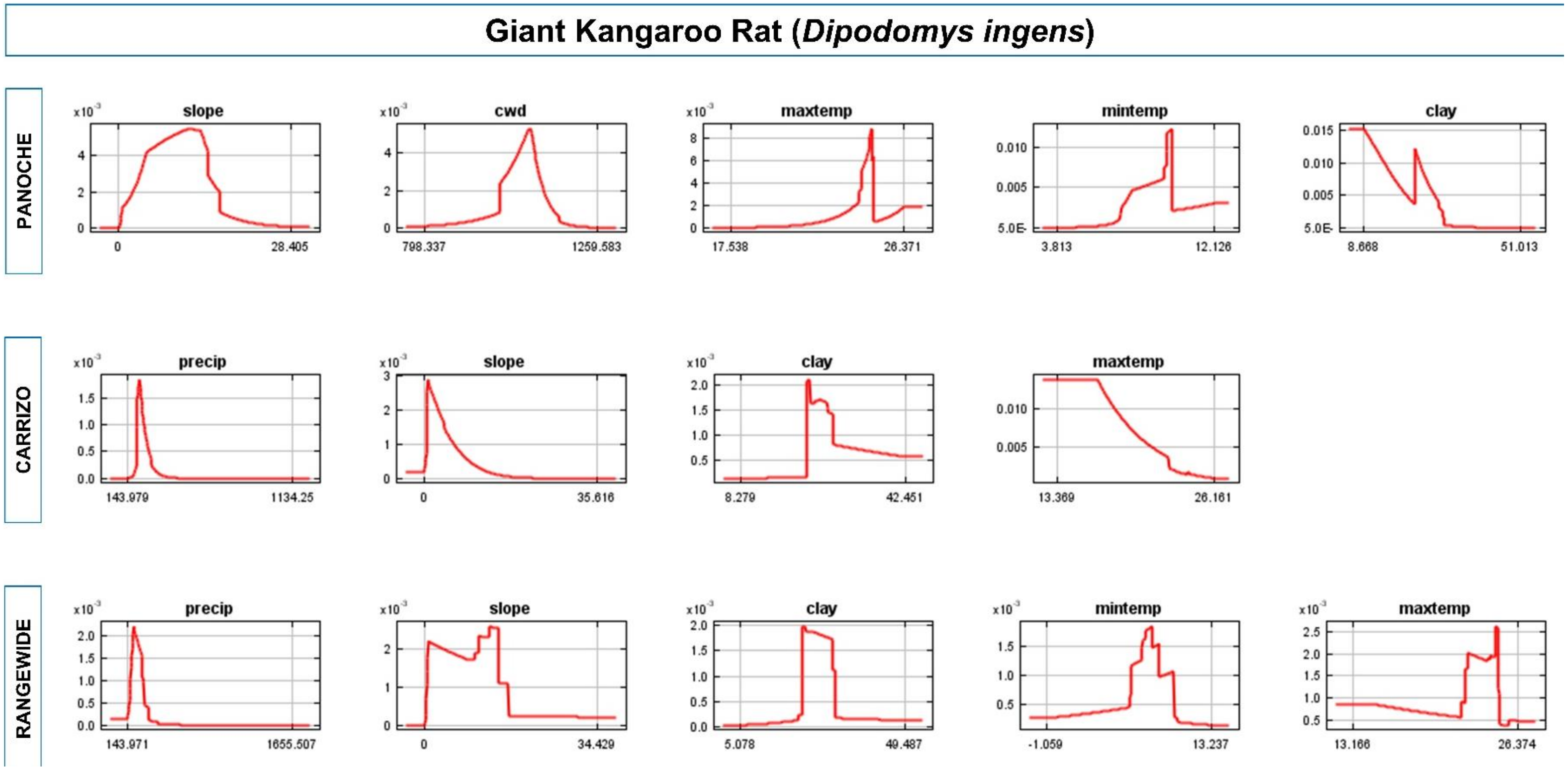
| **Spatial Extent** **Model Variables** | **Panoche** *D. ingens* | **Carrizo** *D. ingens* | **Rangewide** *D. ingens* | **Panoche** *O. beecheyi* | **Carrizo** *O. beecheyi* | **California** *O. beecheyi* |
|---|---:|---:|---:|---:|---:|---:|
| cwd, mintemp, maxtemp, clay | 287 | 72 | 291 | 189 | 2121 | 1292 |
| cwd, mintemp, maxtemp, sand | 361 | 70 | 273 | 98 | 3370 | 901 |
| precip, maxtemp, clay, slope | 193 | 0 | 72 | 205 | 2141 | 429 |
| precip, maxtemp, sand, slope | 284 | 32 | 81 | 114 | 2158 | 420 |
| precip, mintemp, clay, slope | 189 | 7 | 32 | 75 | 2127 | 444 |
| precip, mintemp, sand, slope | 242 | 31 | 18 | 0 | 1975 | 425 |
| precip, mintemp, maxtemp, slope | 158 | 27 | 163 | 219 | 2184 | 393 |
| precip, mintemp, maxtemp, clay | 338 | 71 | 180 | 48 | 2186 | 437 |
| precip, mintemp, maxtemp, sand | 362 | 78 | 191 | 17 | 2160 | 423 |
| maxtemp, clay, slope | 317 | 96 | 604 | 350 | 2385 | 696 |
| maxtemp, sand, slope | 346 | 108 | 594 | 283 | 2374 | 723 |
| mintemp, clay, slope | 298 | 76 | 616 | 363 | 2384 | 722 |
| mintemp, sand, slope | 353 | 113 | 614 | 325 | 2364 | 744 |
| mintemp, maxtemp, slope | 141 | 103 | 512 | 420 | 2412 | 740 |
| mintemp, maxtemp, clay | 336 | 180 | 651 | 259 | 2402 | 897 |

| **Spatial Extent**<br>**Model Variables** | **Panoche**<br>*D. ingens* | **Carrizo**<br>*D. ingens* | **Rangewide**<br>*D. ingens* | **Panoche**<br>*O. beecheyi* | **Carrizo**<br>*O. beecheyi* | **California**<br>*O. beecheyi* |
|---|---|---|---|---|---|---|
| mintemp, maxtemp, sand | 407 | 231 | 631 | 227 | 2624 | 758 |
| cwd, clay, slope | 185 | 34 | 381 | 294 | 2409 | 741 |
| cwd, sand, slope | 242 | 47 | 357 | 207 | 2375 | 732 |
| cwd, maxtemp, slope | 171 | 49 | 377 | 390 | 2815 | 704 |
| cwd, maxtemp, clay | 389 | 75 | 430 | 280 | 2583 | 707 |
| cwd, maxtemp, sand | 443 | 84 | 404 | 208 | 2464 | 691 |
| cwd, mintemp, slope | 171 | 32 | 320 | 355 | 2529 | 687 |
| cwd, mintemp, clay | 307 | 64 | 363 | 183 | 2099 | 750 |
| cwd, mintemp, sand | 395 | 90 | 356 | 93 | 2416 | 707 |
| precip, clay, slope | 291 | 8 | 202 | 264 | 1491 | 437 |
| precip, sand, slope | 329 | 11 | 116 | 192 | 2553 | 213 |
| precip, maxtemp, slope | 295 | 19 | 192 | 365 | 2142 | 463 |
| precip, maxtemp, clay | 450 | 37 | 242 | 214 | 2108 | 278 |
| precip, maxtemp, sand | 517 | 66 | 267 | 147 | 2128 | 416 |
| precip, mintemp, slope | 270 | 26 | 148 | 319 | 2165 | 0 |

| **Spatial Extent**<br>**Model Variables** | **Panoche**<br>*D. ingens* | **Carrizo**<br>*D. ingens* | **Rangewide**<br>*D. ingens* | **Panoche**<br>*O. beecheyi* | **Carrizo**<br>*O. beecheyi* | **California**<br>*O. beecheyi* |
|---|---|---|---|---|---|---|
| precip, mintemp, clay | 411 | 32 | 306 | 74 | 2154 | 424 |
| precip, mintemp, sand | 497 | 77 | 252 | 7 | 2116 | 423 |

# APPENDIX B

Appendix B: Response curves for the top Maxent models at three extents for giant kangaroo rats (*Dipodomys ingens*). Variables are listed from left to right in order of contribution to the model. Variables include percent slope, mean annual climatic water deficit (mm), mean annual maximum temperature ($^{o}$C), mean annual minimum temperature ($^{o}$C), mean annual precipitation (mm), and percent clay. X-axes represents changing values of each variable while all other variables are held constant, and y-axes are the contribution to suitability.



# APPENDIX C

Appendix C: Area under the Curve values for the top five Maxent models from each spatial extent for both species. Models are in descending order of AICc (best model on top) and variables include mean annual precipitation (mm), mean annual climatic water deficit (mm), mean annual minimum temperature (°C), mean annual maximum temperature (°C), percent sand in soil, percent clay in soil, and degree of slope.

| **Species** | **Extent** | **Model Variables** | **AUC** |
|---|---|---|---|
| *D. ingens* | Panoche | cwd, mintemp, maxtemp, clay, slope | 0.981 |
| | | precip, mintemp, maxtemp, clay, slope | 0.980 |
| | | cwd, mintemp, maxtemp, slope | 0.974 |
| | | cwd, mintemp, clay, slope | 0.972 |
| | | cwd, mintemp, maxtemp, sand, slope | 0.976 |
| | Carrizo | precip, maxtemp, clay, slope | 0.971 |
| | | precip, clay, slope | 0.970 |
| | | precip, sand, slope | 0.969 |
| | | precip, mintemp, slope | 0.965 |
| | | precip, mintemp, maxtemp, slope | 0.968 |
| | Rangewide | precip, mintemp, maxtemp, clay, slope | 0.972 |
| | | precip, mintemp, sand, slope | 0.969 |
| | | precip, mintemp, clay, slope | 0.970 |
| | | precip, mintemp, maxtemp, sand, slope | 0.972 |
| | | precip, maxtemp, clay, slope | 0.966 |
| *O. beecheyi* | Panoche | cwd, maxtemp, sand, slope | 0.970 |
| | | precip, mintemp, sand, slope | 0.890 |
| | | mintemp, clay, slope | 0.879 |
| | | cwd, mintemp, sand, slope | 0.859 |

| **Species** | **Extent** | **Model Variables** | **AUC** |
|---|---|---|---|
| | | mintemp, sand, slope | 0.875 |
| | Carrizo | cwd, maxtemp, clay, slope | 0.875 |
| | | precip, clay, slope | 0.882 |
| | | cwd, mintemp, maxtemp, slope | 0.874 |
| | | cwd, mintemp, clay, slope | 0.882 |
| | | precip, mintemp, sand, slope | 0.912 |
| | California | precip, mintemp, slope | 0.957 |
| | | precip, sand, slope | 0.964 |
| | | precip, maxtemp, clay | 0.959 |
| | | precip, mintemp, maxtemp, slope | 0.975 |
| | | precip, mintemp, maxtemp, sand, slope | 0.990 |

# APPENDIX D

Appendix D: Response curves for the top Maxent models at three extents for California ground squirrels (*Otospermophilus beecheyi*). Variables are listed from left to right in order of contribution to the model. Variables include percent slope, mean annual climatic water deficit (mm), mean annual maximum temperature (°C), mean annual minimum temperature (°C), mean annual precipitation (mm), and percent clay, and percent sand. X-axes represents changing values of each variable while all other variables are held constant, and y-axes are the contribution to suitability.