Evaluating current and future range limits of an endangered, keystone rodent (*Dipodomys ingens*)

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**Abstract**

**Aim:** We use current models of species distribution to predict the future habitat suitability for an endangered, keystone rodent (*Dipodomys ingens*, giant kangaroo rat). We incorporate the possibility of local adaptation and novel competitive interactions to improve the predictive accuracy of our Maxent models.

**Location:** San Joaquin Valley, California, USA.

**Methods:** We created Maxent models of two isolated populations of *D. ingens*. Using local surveys and state-wide data, we also modelled 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). We used Warren's *I* to evaluate niche overlap between species as well as between isolated populations of the same species. We then projected each set of models into the future to evaluate *D. ingens* response to climate change.

**Results:** Niche overlap between the *D. ingens* populations was moderate (*I* = 0.44), suggesting that they already experience different climatic regimes and providing support for population-level modelling. Projecting individual populations separately into the future, under a high emission climate change scenario (CCSM4, rcp8.5), resulted in less predicted range contraction than modelling 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.

**Main conclusions:** Modelling the distributions of isolated populations separately provides a more accurate estimation of the species’ contemporary niche, capturing not just overlap between the populations, but individually suitable areas as well. Projecting the individual contemporary and historical models into the future allows us to estimate future habitat suitability. Predicting the distribution of a novel competitor characterizes areas of potential competition. Subsequently, management can target suitable areas for preservation and avoid areas of potential novel competition.

**Keywords**

California ground squirrel, climate change, *Dipodomys ingens*, giant kangaroo rat, interspecific interaction, local adaptation, niche model, *Otospermophilus beecheyi*, small mammal, species distribution model
Climate is often considered the single most important factor limiting species’ ranges (Merriam, 1894; Peterson et al., 2011). Contemporary approaches to modelling 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). Here we define “niche” as the combination of abiotic and biotic factors that a species experiences and those factors’ distribution in geographic space (Hutchinson, 1957). The resulting potential range is the distribution of the bioclimatic envelope, and the realized range is the product of the constraints imposed by biotic interactions (Guisan & Thuiller, 2005). The interaction between abiotic and biotic factors is important in determining whether species follow or deviate from niche conservatism. While coarse-scale studies have detected movements poleward or towards higher elevations, suggesting that species are tracking their climatic niches (Parmesan & Yohe, 2003), long-term and fine-scale studies have revealed more idiosyncratic responses (Gibson-Reinemer & Rahel, 2015; Moritz et al., 2008). Three potential problems with expecting species to exclusively track their contemporary, realized, abiotic niche are as follows: (a) most studies focus on temperature without regard to precipitation (Rapacciuolo et al., 2014); (b) populations may have adapted to local climate regimes (Gibson-Reinemer & Rahel, 2015); and (c) species may be constrained by biotic factors that are only currently correlated with abiotic proxies (Guisan & Thuiller, 2005).

Abiotic factors are commonly used in distribution and niche modelling (Aycrigg et al., 2015; Beaumont et al., 2016; Escalante, Rodríguez-Tapia, Linaje, Illoldi-Rangel, & González-López, 2013; Lawler, White, Nielson, & Blaustein, 2006). Climate-driven models of species distributions have received criticism for focusing on temperature without consideration of precipitation (Rapacciuolo et al., 2014). Precipitation helps shape the vegetative community, directly affecting primary productivity, a major limiting factor for many species (Brown, Reichman, & Davidson, 1979). More recent work has suggested that precipitation may be as important as temperature in limiting species’ range shifts (Tingley, Monahan, Beissinger, & Moritz, 2009).

Even with the improved accuracy from multiple climatic variables, broad correlations between species distributions and climate may obscure local adaptations. Some species’ ranges may shift to track a fluctuating niche, while other species’ ranges remain in place, exposing them to changes in climate (Holt, 1990). Non-contiguous populations within a species could experience dissimilar climatic conditions, and over time, the population-level niche could vary based on local conditions (Gibson-Reinemer & Rahel, 2015). Modelling genetically unique subpopulations should improve the predictive accuracy of distribution models (Gonzalez, 2011).

Considering multiple aspects of climate may make predictions more accurate but neglects the potentially powerful influence of biotic interactions (Post, 2013). 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 (Boulangeat, Gravel, & Thuiller, 2012; Gaston, 2003). Climate change is expected to affect community assembly, with species expanding across community boundaries at different rates, inducing novel competitive interactions (Montoya & Raffaelli, 2010). 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 & Thuiller, 2005). However, because species respond to climate change at various temporal scales and via different mechanisms, the relationship between climate and competition may be decoupled when projecting into the future (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Lurgi, Lopez, & Montoya, 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 in species distribution modelling. *D. ingens* are a state and federally listed endangered species endemic to California’s Great Central Valley, a global biodiversity hotspot (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000; USFWS, 1987). They currently only reside in a few remnant and 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 ~150 km, and recent work suggests deep genetic isolation dating back at least 6,000 years, making local adaptation more likely (Statham, Bean, Alexander, Westphal, & Sacks, 2019). Although these populations may experience different local conditions, the species exists within a narrow range of habitat characteristics (Bean, Stafford, Butterfield, & Brashares, 2014). These habitat specialists thrive in desert-grasslands with low annual precipitation (<30 cm), sandy loam soils, and flat or very low-grade slopes (Grinnell, 1932; Hawbecker, 1951). 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 & Brashares, 2012). They are thus considered ecosystem engineers and a keystone species (Prugh & Brashares, 2012). Understanding the limitations to *D. ingens* range will 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, Stafford, et al., 2014). Persistence in areas of low annual precipitation is 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 are undetermined (Bean, 2012). *D. ingens* could be limited by precipitation in several ways, leading to three non-exclusive...
mechanistic hypotheses. First, as a burrowing, seed-caching species, high precipitation could directly affect their ability to maintain burrows, or cause seed spoilage, depleting seasonal food stores (“Precipitation” hypothesis, Valone, Brown, & Jacobi, 1995). Second, 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 (“Vegetation” hypothesis, Germano, Rathbun, & Saslaw, 2012). Climatic water deficit combines the effects of precipitation, temperature and radiation to provide a metric of available water (Flint & Flint, 2014). A lower deficit would result in increased soil moisture, which could improve growth conditions for dense non-native vegetation, inhibiting saltatorial movements (Stephenson, 1998). Finally, while D. ingens is considered competitively dominant within its community, wetter areas of their range are suitable to potential novel competitors (“Competition” hypothesis, Grinnell, 1932; Prugh & Brashares, 2012; Bean, 2012). 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 with this aggressive species could result in antagonistic interactions (Trulio, 1996). In fact, Williams, Germano, and Tordoff (1993) observed O. beecheyi raiding D. ingens seed caches and report anecdotal evidence of a direct mortality or eviction event of D. ingens due to burrow invasion. 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 (Eastman, Morelli, Rowe, Conroy, & Moritz, 2012; Grinnell & Dixon, 1918; Hubbart, 2012; Moritz et al., 2008). We investigate this species particularly because of its life history and current apparent distribution that create its potential for competition. As the largest of the kangaroo rats, D. ingens dominates its current community, thus we suggest that it would require a larger, more aggressive species to interrupt or displace this hierarchy. While D. ingens may encounter a suite of novel interactions with other species, O. beecheyi, according to current conditions, appears to be the most likely.

The Carrizo and Panoche populations experience different climatic regimes—the Panoche receives 100 mm (~45%) greater average annual precipitation than the Carrizo. It is therefore possible that the two populations of D. ingens adapted to their respective local conditions. This could reduce niche overlap between populations, but predict less range contraction, given the populations are adapted to a wider range of climatic conditions.

To test three hypotheses of D. ingens range limitation, we identified important variables in species distribution models. By incorporating more direct mechanisms—that is local adaptation and biotic interactions—we attempted to improve the predictive accuracy of habitat suitability from species distribution models for D. ingens. We 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, we compared the rangewide model (1) to the population-level niche models (2 and 3) to determine differences of population-level models. Then, we used the Panoche and Carrizo models to project the population-level estimates of habitat suitability rangewide, for both current and future climate. Finally, we estimated niche overlap between D. ingens and O. beecheyi to assess the possibility of a competitive interaction limiting D. ingens range expansion. To understand how different approaches to modelling contemporary range limits might impact future climate projections and to inform future management, we projected the top performing models into the future.

2 | METHODS

2.1 | Study area

The San Joaquin Valley, the southern portion of California’s Great Central Valley, is a desert characterized by mild winters with low rainfall, and hot, dry summers (Germano et al., 2011). Much of the land includes agriculture and oil development that has replaced D. ingens habitat and is also at risk for solar energy development (USFWS, 2010; Williams et al., 1998).

The northern population of D. ingens persists in the Cievaro-Panoche Natural Area (“Panoche”) in San Benito and Fresno Counties (Figure 1). While this population’s habitat is the more mesic Central Valley, is a desert characterized by mild winters with low precipitation and hot, dry summers (Germano et al., 2011). Much of the land includes agriculture and oil development that has replaced D. ingens habitat and is also at risk for solar energy development (USFWS, 2010; Williams et al., 1998).

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Throughout their range, D. ingens are sparsely distributed on the locally available areas of level terrain or gradual slopes.

In California, the average annual temperature has increased 1.7°C over the last century, 70% higher than the U.S. national average (Moser, Franco, Pittiglio, Chou, & Cayan, 2009). During this time, the state also experienced extended periods of drought (National Drought Mitigation Center, 2016). The maximum temperature in the Panoche is expected to increase between 2.5 and 4.1°C by the years 2070–2099. Annual rainfall is expected to remain stable or to increase by up to 28 mm; 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 30 and 38 mm (Cal-Adapt, 2016).

2.2 | Data collection

2.2.1 | Live trapping

Occurrence data came from trapping across the range in 2010–2017. Target-based trapping consisted of using extra-long Sherman live traps to identify the presence of D. ingens at sites with occupancy signs, such as burrows mounds or scat. Trapping protocol followed Prugh and Brashares (2010) and Alexander (2016). For modelling purposes, presence was recorded at the site level to reduce autocorrelation and to be more appropriate for the scale of the environmental variables. All work was performed under Humboldt State Animal
Care Protocols 13-14.W.109-A and 16/17.W.96-A and followed American Society of Mammalogists guidelines (Sikes et al., 2011). Our trapping locations included 197 presences in the Panoche, 101 in the Carrizo, and 334 rangewide, covering much of the range of *D. ingens*. However, we were unable to acquire observed presences in the Lokern and Elk Hills regions, areas of known GKR occupancy. We therefore supplemented our data with 33 occurrences from the California Natural Diversity Database (CDFW, 2018).

2.2.2 | Environmental variables

We acquired climatic data from the Basic Characterization Model (Flint & Flint, 2014). We 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 modelling, about 900 m (Table 1). While this scale is a product of data availability, it is also appropriate for modelling this species because individuals have a home range of about 200–1,000 m² (Cooper & Randall, 2007). This means that one cell could represent the environmental variables selected by an individual, or a group of individuals, which we classify as a site.

2.2.3 | Driving surveys

In 2017, we conducted driving surveys to record sightings of *O. beecheyi*. Due to logistics of travelling between the two populations, we were restricted to strategically surveying only one population extent. We considered the Panoche population of *D. ingens* to be at the greatest risk of competition with *O. beecheyi*, and thus, we drove our surveys within a 50 km radius of the Panoche (Figure 1). With an additional observer, we 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, 281–390, 391–500, 501–610, 611–720 mm), and overall, the survey contained approximately equal numbers of survey points among these zones (Flint & Flint, 2014). Surveys occurred every 4 km along the survey route. Two observers used binoculars to search the 360° visual field surrounding the survey point for O. beecheyi for 2 min (Downey, 2003). We estimated that, due to topography and land use, even the greatest distance from the survey point to a squirrel detection was within a 900 m pixel. If a squirrel was detected before the 2 min were complete, the point was coded as a presence and the survey continued to the next location. Opportunistic ground squirrel sightings during the surveys and during D. ingens trapping were also recorded.

### 2.3 Species distribution modelling

We used Maxent to create species distribution models for D. ingens and O. beecheyi (Phillips, Anderson, & Schapire, 2006). Maxent is a machine-learning algorithm that calculates the maximum entropy probability distribution of occurrence points under a set of environmental constraints. It assumes that the distribution of a given species is driven by some combination of this set of environmental variables and can explore complex relationships between them. Maxent is useful for studying rare and declining species because it requires the input of only presence locations and performs well with small data sets. Maxent thins presence locations by interpreting a single point per pixel, according to the resolution of the input variables, reducing the risk of autocorrelation. Maxent samples background locations (default = 10,000) to compare to these presence locations. No inference is made as to whether background locations are presence or absence sites, hence they are considered “available.” Once a model is estimated, Maxent projects it to the entire study area, resulting in a map of values ranging from zero to approximately one. These values have multiple interpretations, but not all are appropriate for every species. For the purposes of this study, Maxent values are referred to as habitat suitability. Bean, Prugh, et al. (2014) found that Maxent accurately predicts long-term habitat suitability for D. ingens at a coarse temporal scale, which is appropriate for our species and environmental data.

We 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 (rcp8.5) (Gent et al., 2011). We chose to model the future predictions under this pathway to capture the greatest potential change. Lower emissions scenarios could underestimate the potential impact of climate change and rcp8.5 allows us to compare the current model to the riskiest scenario, which may be more likely to occur depending on current and future policy changes and political climates.

For current climatic conditions, we created species distribution models for three subsets of the D. ingens range: Pancho, Carrizo and a rangewide model that contained both populations. After selecting biologically relevant predictor variables, we decoupled predictor variables with |r| greater than 0.7, meaning the variables remained as possible environmental predictors, but were not paired in a single model (Pearson, 1920). Mean annual temperature was highly correlated with all but the soil characteristics and was thus removed as a predictor. Using a jackknife test of variable importance and each variable’s per cent contribution to the models, we finalized the set of variables available for candidate models (Table 1). Aspect was removed from the final candidate model set for lack of contribution in preliminary model evaluation. We adjusted the beta value, a regularization parameter designed to optimize data fitting, on the preliminary models (β = 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 β = 1, and thus, we determined that this value was the most appropriate (Morales, Fernández, & Baca-González, 2017). We used the default auto-features setting to select feature types and selected the complementary log-log

| Variable | Relevance | Source | Spatial resolution (m) | Temporal resolution |
|----------|-----------|--------|-----------------------|--------------------|
| precip  | Mean annual precipitation | Forage availability, food spoilage | Basin Characterization Model (Flint & Flint, 2014) | 270 | 1981–2010 |
| cwd     | Mean annual climatic water deficit | Forage availability, locomotion | Basin Characterization Model (Flint & Flint, 2014) | 270 | 1981–2010 |
| mintemp | Mean annual minimum temperature | Foraging time, forage type | Basin Characterization Model (Flint & Flint, 2014) | 270 | 1981–2010 |
| maxtemp | Mean annual maximum temperature | Foraging time, forage type | Basin Characterization Model (Flint & Flint, 2014) | 270 | 1981–2010 |
| sand    | Mean per cent sand in soil | Burrowing | Soil Survey Geographic Database (NRCS, 2003) | 900 | 2003 |
| clay    | Mean per cent clay in soil | Burrowing | Soil Survey Geographic Database (NRCS, 2003) | 900 | 2003 |
| slope   | Degrees of slope | Burrowing, locomotion | US Geologic Survey (USGS, 2013) | 30 | 2013 |

Note. All variables were resampled to the coarsest resolution.
output for Maxent predictions, constraining the output values between zero and one. With these constraints, we constructed a final candidate model set of 43 different combinations of the seven variables for model selection (see Supporting Information Table S1.1 in Appendix S1).

The best model for each geographic subset was chosen using AICc, and model discrimination ability was assessed using area under the curve (AUC) and the Continuous Boyce Index (CBI; Hirzel, Lay, Helfer, Randin, & Guisan, 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, Vernier, Nielson, & Schmiegelow, 2002). We calculated CBI using ten bins with a moving window between the maximum and minimum suitability values. We used 75% of the data to train the model and 25% to test using CBI. The result was a value between negative one and one, where a positive one represents a model that perfectly predicted presence, zero means the model is no better than random chance, and negative values predicted presence in the areas of the lowest suitability (Hirzel et al., 2006).

Due to habitat loss, a contemporary model may not capture the full range of the environmental niche. A.L. Rutrough (personal communication) 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, we projected the model of historical distribution into the future. Then, based on habitat suitability, we compared the predicted range contraction from our new models to that of the historical model. An estimate of historical niche breadth should be broader than the contemporary model. The historical model included 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 modelling process was then repeated with *O. beecheyi* occurrence data to create a similar suite of distribution models. The models included presence locations from opportunistic sightings, driving surveys, and GBIF, an open access resource for biodiversity data (Global Biodiversity Information Facility; GBIF Secretariat, 2017a, 2017b). We modelled three geographic extents, slightly different from the *D. ingens* models: California-wide (421 GBIF locations)—rather than rangewide—and locally within the Panoche (165 survey locations) and Carrizo (34 survey locations). We used only GBIF locations to create the California-wide models, to avoid over-sampling our study areas. For the Panoche and Carrizo models, we included survey locations and anecdotal sightings, but thinned the locations using the geogThin function in R package “emmdsm” so that clusters of squirrels within one pixel were represented by a single location (Muscarella et al., 2014; Smith, 2018).

To visualize contemporary and future distributions and inform management, we selected threshold values to convert continuous habitat suitability maps to models 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. We subdivided suitability into two categories, low and high. We considered “low” suitability to be between the 5th and 50th percentile, and all greater values were considered “high” suitability. We used the same values for thresholding future models. These threshold values were only used for mapping purposes; un-thresholded models were used for further analyses.

### 2.4 | Niche overlap

The top *D. ingens* population models were compared to evaluate niche overlap as evidence for separate adaptation. Subsequently, overlap between the same models was calculated based on future climate projections. Low niche overlap would indicate that populations experience different environmental regimes and could suggest adaptation. We used Warren’s I (Warren, Glor, & Turelli, 2008) to calculate the degree of niche overlap, a commonly used strategy for evaluating niche conservatism using habitat suitability models (Wiens et al., 2010). This similarity statistic assumes that habitat suitability is an appropriate measure of the niche, which is reasonable for our coarse temporal scale with distinct differences in each population’s environmental variables (see Supporting Information Figure S2.2 in Appendix S2). Warren’s I ranges from zero to one, with a value of one indicating identical niche models. These calculations were conducted using the “ENMeval” package in R (Muscarella et al., 2014). We also evaluated niche overlap by calculating the CBI of each population’s model projected into the other population’s geographic extent, where a negative CBI value would indicate low niche overlap. Low overlap between populations would indicate that they experience different environmental regimes. 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 estimate 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 increase in the future.

### 3 | RESULTS

#### 3.1 | Species distribution modelling

##### 3.1.1 | *Dipodomys ingens*

The top models for two of three geographic extents were unambiguous; all other models had ΔAICc greater than seven (see Supporting Information Table S1.1 in Appendix S1). For the Carrizo model, there were two models within seven AICc, but we chose the model with the lowest AICc value. The Panoche model included climatic water deficit, minimum temperature, maximum temperature, per cent clay and slope (Table 2, Figure 2). The Carrizo model included precipitation, maximum temperature, per cent clay and slope (Table 2, Figure 2). The rangewide model...
including precipitation, minimum temperature, maximum temperature, clay and slope (Table 2, Figure 3). The response curves indicated selection for low slope, high minimum temperature, low precipitation and a peak in suitability around 23% clay in the soil (see Supporting Information Figure S3.3 in Appendix S3). All top models had AUC scores above 0.9 (see Supporting Information Figure S4.4 in Appendix S4). The CBI values were also all above 0.9. Figures reflect suitability values in which 95% of detections occurred (5th percentile threshold, suitability > 0.18, 0.18 and 0.11 for the Panoche, Carrizo and rangewide, respectively). This threshold value was selected based on where the majority (95%) of presence locations occur within each model projection. These

|        | Precip | CWD | Min Temp | Max Temp | Sand | Clay | Slope |
|--------|--------|-----|----------|----------|------|------|-------|
| Panoche| 31     | 13  | 16       | 7        | 33   |      |       |
| Carrizo| 45     | 9   | 4        | 42       |      |      |       |
| Rangewide| 46   | 9   | 5        | 33       |      |      |       |
| Panoche| 35     | 9   | 51       | 5        |      |      |       |
| Carrizo| 30     | 3   | 9        | 58       |      |      |       |
| California| 65  | 17  |          |          |      |      |       |

Note. 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 per cent 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 per cent sand in soil, mean per cent clay in soil and degrees of slope.

**FIGURE 2** Current (1980–2010) and future (2070–2099) species distribution models for giant kangaroo rats (*Dipodomys ingens*). Models were trained locally and projected rangewide, San Joaquin Valley, California. 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 grey 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

**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*)
values were only used for map construction, making viewing of three separate models with the same extent possible in a static image. However, all analyses were performed using the full models.

When populations were modelled together in the rangewide model, the prediction of future habitat suitability was low and covered an extremely small area (Figure 3). However, when the two populations were modelled separately and each projected into the future (2070–2099), less range contraction was predicted (Figure 2). The future projection of the historical model also predicted far less range contraction than the rangewide model (Figure 4).

3.1.2 | Otospermophilus beecheyi

The top models for all three extents—Panoche, Carrizo and California-wide—differed but were unambiguous (Table 2, Figure 5). Habitat suitability for all extents included a strong effect of low slope. Other trends include increased suitability at high temperatures and low precipitation (see Supporting Information Figure S5.5 in Appendix S5). All models had AUC values above 0.8 (see Supporting Information Figure S4.4 in Appendix S4) and CBI values for the Panoche and California were 0.99 and 0.91, respectively, while the CBI for the Carrizo was 0.79.

3.2 | Niche overlap

All D. ingens models were positively correlated. When calculating CBI to compare the Panoche model's ability to predict suitability in the Carrizo, the values were well below zero, at about −0.8, indicating these models predicted the highest suitability in the least suitable areas. CBI for the Carrizo model in the Panoche extent was about 0, indicating that the model is no better than a random model at predicting the northern population’s suitability. Niche overlap between the current Panoche and Carrizo populations was moderate (Warren’s $I = 0.44$). Niche overlap between O. beecheyi and D. ingens in the Panoche was higher than overlap between species in the Carrizo (Figure 6). Although the models of niche are consistent from current to future, the geographic availability of combinations of environmental factors changes, allowing for different levels of niche overlap in the future. Niche overlap decreased between D. ingens

![FIGURE 3](image-url) Current (1980–2010) and future (2070–2099) species distribution models for giant kangaroo rats (Dipodomys ingens). Models were trained rangewide (San Joaquin Valley, California) including all presence locations. Higher suitability is indicated by darker shading. The grey 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
I increased in the future (however, overlap between the Panoche population andJoquin Valley. We believe this translates into a useful prediction of

crosshatching shows areas of agriculture or residential use. San

FIGURE 4 Future (2070–2099) species distribution model for
giant kangaroo rats (Dipodomys ingens), based on their historical
distribution. A.L. Rutrough (personal communication) 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 grey shading indicates the
historical distribution presented by Williams et al. (1992), and the
crosshatching shows areas of agriculture or residential use. San
Joaquin Valley, California

populations in the future (I = 0.44–0.37). Niche overlap between the
Carrizo population and O. beecheyi also decreased (I = 0.58–0.53); however, overlap between the Panoche population and O. beecheyi
increased in the future (I = 0.63–0.74) (Figure 6).

4 | DISCUSSION

Our models of local, contemporary D. ingens habitat suitability
more accurately reflect the true distribution represented in the San
Joaquin Valley. We believe this translates into a useful prediction of
future habitat suitability. When populations were modelled together,
a single, rangewide model predicted extreme future range contra-
tion, with almost complete extirpation from their current range.
However, population-specific modelling provided a more optimistic
forecast. The future prediction of the historical model, which re-

used in combination, these models highlight areas of consistently
suitable habitat, taking into account historical niche, as well as local
adaptation. The areas of overlap likely represent patches appropri-
ate for conservation prioritization.

Species distribution models of D. ingens in the past have focused
on rangewide or Carrizo-specific models, leaving the Panoche pop-
ulation relatively underrepresented (Bean, Stafford, et al., 2014).
Habitat destruction and climate change have contributed to range
contraction, isolation and potentially local adaptation. The two
populations currently experience significantly different ranges of
the same environmental variables (see Supporting Information
Figure S2.2 in Appendix S2). Our comparison of D. ingens local and
rangewide models revealed niche differences between populations,
providing evidence that the two populations should be treated sep-
arátely. A.L. Rutrough (personal communication) created a historical
distribution model which we projected according to current climatic
conditions. Using the historical model to predict current habitat suit-
ability, the Carrizo was predicted to remain relatively stable, but the
Panoche was predicted to decrease in suitability. Hence, the per-
sistence of D. ingens in the Panoche is an indicator of adaptation
through time and supports the increased local accuracy of popu-
lation-specific models. Our 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,
a concept supported by a review of range shifts written by Gibson-
Reinemer and Rahel (2015).

For D. ingens, the environmental factors included in the top local
models were similar for both populations and consistent with previ-
sous literature (Bean, Stafford, et al., 2014; Grinnell, 1932; Williams,
1992), with the exception of the precipitation variable. The limita-
tion imposed by precipitation could be defined by either excessive
or insufficient rainfall. In the Carrizo model, precipitation was an in-
fuential variable, contributing 45% to the model (Table 2). Excessive
precipitation may cause direct effects of water infiltration and bur-
row collapse (Germano, Rathbun, & Saslaw, 2001). Alternatively,
precipitation could better define the areas limited by too little water,
hindering primary productivity. The Panoche model included cli-
matic water deicit 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. Tingley et al. (2009) compared niche shifts of 53 bird
species from historical (1911–1929) to contemporary (2003–2008)
ranges, showing that species’ responses to changing climate could
not be predicted solely from temperature or precipitation, but esti-
mates were far more accurate when the two were used in tandem.

The local models predicted far less range contraction than the
rangewide model. However, the historical model, which modelled
the species’ historical environmental niche, predicted even less
range contraction than the local models. This could be because it
represents a broader niche breadth, capturing suitable areas where
D. ingens has been extirpated due to human development. Because
the modern projection of this historical model does not match the
available habitat, modelling the populations separately could better capture the current range of suitable environmental conditions. 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 2).

Moderate niche overlap between populations indicated some niche divergence. The local models indicated retention of some niche characteristics shared between populations (i.e. low slope) but emphasize the developed variation between them, such as the importance of climatic water deficit over precipitation in the Panoche. These differences in climatic factors could alter their response to environmental change and disparate reactions to species interactions. Although previous work (Good, Williams, Ralls, & Fleischer, 1997; Loew, Williams, Ralls, Pilgrim, & Fleischer, 2005) found relatively low genetic differentiation in neutral microsatellites between the Panoche and Carrizo,
The areas of niche overlap between the local species models in the Panoche, the population of greatest concern for competition, are within confirmed current *D. ingens* habitat, including areas where the two species have been observed in close proximity (Figure 5). 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 our findings, such interactions warrant future study.

Because niche overlap was predicted to decrease between future populations, management should focus on protecting locally suitable areas. Hence, treating populations similar to those in a subspecies 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 was 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*.

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. Modelling the contemporary distribution likely represents the current realized niche for both populations, and thus, the future predictions assume the restrictions placed on the populations will persist and relationships to environmental variables will be maintained. Additionally, land use and vegetation type were not included in the modelling process because there are no known spatially explicit projections of land use for this region of California. While we did not directly model the effect of *O. beecheyi* in future range predictions, niche overlap was expected to increase in the Panoche, creating more potential for competition. In the future, incorporation of these key elements would create a more accurate model, improving the predictions of future ranges.

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. 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 7). 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.
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 7). 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 Pancho Valley on the western edge of the Pancho (Figure 7). This area is threatened by solar development but remains one of the most suitable areas for both populations. 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. Our models do not include individual biotic factors that estimate the ability of populations to reach areas of high suitability (see Alexander, 2016 for connectivity modelling of D. ingens). We can however use life history knowledge in combination with these models. D. ingens has a relatively short dispersal distance (~2.5 km, 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. heermannii, 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).

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 modelling (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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DATA ACCESSIBILITY

As the raw information represented in the figures pertains to a listed endangered species, it is not publicly available. However, raster layers of the models are available to managers and the scientific community upon request.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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