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Reconsidering habitat associations in the Anthropocene

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A R T I C L E I N F O

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A B S T R A C T

The California ground squirrel (*Otospermophilus beecheyi)* is generally undervalued despite serving as an ecosystem engineer in grassland ecosystems. Evidence of significant engineering effects by squirrels indicates that population reductions have cascading effects on other species, including several conservation-dependent species. While the theory and practices behind habitat association studies are already well established, our application of this approach helped identify priority management options in degraded grasslands expected to change further under shifts in climate. In this study we conducted surveys for California ground squirrels throughout San Diego County grasslands and examined habitat covariates to determine the ecological variables currently associated with occurrence. The primary objectives were to 1) improve our understanding of the habitat variables associated with squirrel presence, and 2) develop a predictive model for squirrel habitat suitability at a local scale. The most predictive models included significant main effects for percent sand (as a component of soil texture) and vegetation cover. A 10% increase in vegetation cover was associated with 1.3 fold lower odds of squirrel presence, whereas a 10% increase in percent sand was associated with 2.0 times higher odds of squirrel presence. Comparison of the predictive accuracy of soil texture data at two scales (fine-scale field vs. landscape scale GIS layers) showed fine-scale field sampling has greater predictive strength. Because soil type is a logistically non-malleable factor for wildlife managers, it is important to categorize management sites by soil type to identify the potential for promoting fossorial species on the landscape. With the prospect of shifting landscape ecotones due to climate change, it is as important to understand the basic habitat requirements of keystone species as for rare species.

1. Introduction

Recently, increased importance is being assigned to the conservation value of non-endangered species that nonetheless exert disproportionate influences on ecosystem function and thus help maintain systems for conservation-dependent species (Byers et al., 2006; Delibes-Mateos et al., 2011). Fossorial mammals are undervalued but important species, which due to their abundant populations, help shape and maintain extensive grassland ecosystems, foster heterogeneity of habitats at the landscape level, and maintain biodiversity (Davidson et al., 2012). Fossorial mammals, particularly rodents, exert numerous influences over the abiotic and biotic components of grassland communities. The extensive burrowing activity of burrowing

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mammals results in increased soil temperature, nutrient availability, and water infiltration (Schiffman, 2007), which increases the foraging quality of surrounding vegetation. This cyclical relationship creates a positive feedback that contributes to the continued viability and persistence of healthy grassland communities at all trophic levels. It also creates patches of grassland with vegetation and wildlife assemblages that vary distinctively from adjacent areas (Davidson et al., 2012).

Unfortunately, many small mammal species that serve as ecosystem engineers are persecuted as pests and have suffered large declines in abundance, but rarely figure prominently in conservation planning and policy (Delibes-Mateos et al., 2011). Population reductions in burrowing mammals result in cascading effects on other plant and animal species that rely heavily on their presence, such as the conservation-dependent burrowing owl (*Athene cunicularia hypugaea*; Davidson et al., 2012). Thus, an undervalued tool for conservation includes the protection and restoration of ecosystem engineers that help create desired system states that are consistent with conservation goals (Byers et al., 2006; Delibes-Mateos et al., 2011). Species that play a disproportionate role in shaping ecosystems may further address other conservation problems, potentially conferring ecological resilience to global climate change through their stabilizing ecosystem engineering effects (Allen et al., 2011).

The foundation for the management of ecosystems using ecosystem engineers rests on a clear understanding of the habitat requirements for the species, as evinced in evidence-based approaches to conservation management (Sutherland et al., 2004). Habitat suitability modeling is a powerful tool for guiding management actions to the most promising geographic locations to support recovering populations of rare or threatened species (Mateo-Tomás and Olea, 2010). These models require rigorous data on the habitat associations of the species of interest or they can be misleading, particularly for species with unstable distributions, as is often observed in threatened or persecuted species (Cianfrani et al., 2010; Güthlin et al., 2011). However, approaches to identifying and managing suitable habitat in the highly altered environments of the Anthropocene require revisionist thinking. We must remain open to inclusion of novel and invasive ecosystem components if they are unlikely to be reversed and are being utilized beneficially by some native species (Corlett, 2015). The resulting ecosystems will not be pristine, but as Corlett (2015) suggests, many ecologists would agree that "… saving species from extinction and maintaining resilient, functioning ecosystems are still worthwhile goals on a human-dominated planet." Grasslands today are dramatically different from those present hundreds of years ago, and comprise a hybrid mixture of historical and novel components (sensu Hobbs et al., 2009). Burrowing engineers could help maintain hybrid combinations of historical native species of value and the inevitable novel components.

As a species that is frequently observed in community parks and agricultural landscapes, the California ground squirrel (*Otospermophilus beecheyi*) is generally undervalued and designated a "pest" species. Systematic eradication efforts, habitat destruction, and introduction of non-native species have led to the reduction of ground squirrel populations throughout their historic range, with numbers too low to adequately perform their role as ecosystem engineers (Lenihan, 2007). The historical prevalence of ground squirrels was documented in numerous historical sources such as the journals of early explorers and naturalists, which describe widespread extents of grassland so perforated with burrows that crossing them on horseback was dangerous (Schiffman, 2007). Other species, such as the pocket gopher (genus *Thomomys*), were also widespread and have obvious impacts on ecosystem function, but the burrows are much smaller in size. The presence of California ground squirrels and their burrows is associated with a greater diversity and abundance of some types of species and a reduction in other species, yielding a mosaic habitat that is overall more diverse (Lenihan, 2007). Although not yet robustly evaluated for its ecosystem engineering role, the burrowing activity and vegetation impacts of California ground squirrels (Lenihan, 2007; Schiffman, 2007) creates physical effects that are distinct from those caused by strictly abiotic processes and are quantifiably large relative to the effects of physical processes occurring in the system, thus appearing to meet conservative criteria for ecosystem engineer status (Reichman and Seabloom, 2002).

The California ground squirrel is one of the most numerous and visible occupants of California grasslands (Schiffman, 2007), which are themselves among the most endangered ecosystems in the temperate world (Samson and Knopf, 1996). In California, approximately 90% of species listed in the Inventory of Rare and Endangered Species can be found in grasslands (Barry et al., 2006). Further, the interaction of climate change and development pressure are impacting native species in tandem (Jongsomjit et al., 2013) and greater dominance of non-native plant species is predicted for the region (Sandel and Dangremond, 2012). To the extent that grounds squirrel help engineer and stabilize this system, a holistic management program for California grasslands must include efforts to maintain or restore levels of California ground squirrels, yet surprisingly little research addresses habitat associations of ground squirrels and most past research has been highly localized to specific ecological contexts (Ordeñana et al., 2012).

To address this dearth of information for an important ecosystem engineer, we developed a comprehensive study of the factors influencing habitat suitability for the California ground squirrel in Southern California native and non-native grasslands. An understanding of why ground squirrels are locally abundant at some sites while absent at others is necessary to promote the successful selection of sites that have the best potential for successful attempts at translocation or natural dispersal. In this study we conducted surveys for California ground squirrels and examined habitat covariates from fine-scale field data and broad-scale GIS data to determine the ecological variables currently associated with their distribution and relative abundance. An adequate evaluation of habitat factors that influence animal distribution requires research carried out over both broad and fine ecological scales because habitat selection is influenced by a hierarchy of habitat factors ranging from regional to microhabitat scales (George and Zack, 2001). Our primary objectives were to 1) improve our understanding of the habitat variables associated with squirrel presence and 2) develop a predictive model for squirrel habitat suitability at a local scale. We pursued these objectives with a view to establish current local baselines in rapidly changing grasslands and help predict and mitigate against further perturbation from climate change.

2. Methods

2.1. Study area, grassland surveys, and soil texture

The study area consisted of 16 grasslands sites throughout San Diego County selected based upon the following criteria: 1) classified as a grassland ecosystem, 2) elevation of less than 1200 m (m), and 3) minimum size of 10 ha. Grasslands in San Diego County are typically dominated by dense cover of non-native annual grasses and forbs. Common grassland species encountered included wild oat *(Avena* spp.*),* ripgut brome *(Bromus diandrus)* and compact brome *(Bromus madritensis)*; non-native species of forbs included storksbill *(Erodium* spp*).* Shrubs and trees occurred at varying frequencies across study sites, and typically included coastal sage scrub species such as California buckwheat (*Eriogonum fasciculatum*) and chamise (*Adenostoma fasciculatum*), along with woodland species like coast live oak (*Quercus agrifolia*). Sites also varied with regard to historical land-use patterns, primarily farming and grazing. While some sites had no current active vegetation management, other sites had various types and levels of management, including cattle grazing and prescribed burns.

We conducted California ground squirrel burrow surveys during May–July 2012 and April–July 2013. The location and orientation of fifteen 50 m long belt transect survey lines were generated using ArcGIS 10.3 at all sites with the exception of three sites: JM (n = 13), RP (n = 7), and PR (n = 13), due to constraints in site configuration. Origin points for the transects were generated randomly in ArcGIS within an area of interest polygon for each site. A random number generator in ArcPy was used to generate the bearing angle for each transect from an azimuth between 1 and 360. Transects were then extended out 50 m from each origin point on the bearing angle, with a minimum distance between transects set at 25 m. We scanned the transect to a distance of 2 m on either side of the center line, for a total belt width of 4 m. We surveyed squirrel burrows rather than squirrels themselves, to make surveys more efficient and virtually eliminate problems associated with squirrel detectability. While burrow numbers are not directly indicative of squirrel numbers, burrow entrances serve as a good index of squirrel abundance (Owings and Borchert, 1975; Ordeñana et al., 2012). Burrow surveys have the added benefit of sampling the chief squirrel-mediated habitat effect beneficial to native grassland species. Squirrel burrows were identified by an entrance with a diameter of 7 cm or greater. Indicators of recent activity such as presence of squirrel feces, latrines, and fresh digging, as well as direct observations of squirrels, were noted. If at least one burrow was detected, we established a 10 × 10 m plot (squirrels present) with the burrow at plot center. If we failed to detect a burrow along the transect, we established a control plot (squirrels absent) centered at meter 45 on the transect line. All 10 × 10 m plots had a north-south orientation.

We collected the following data at each habitat plot: GPS location of plot-center/burrow; elevation (m); percent slope and aspect; and site history (grazing/burn), if known. Active burrows were defined by the presence of fresh digging, collected seeds, and/or squirrel feces and recorded. Ten 10 m point intercept transects were established within the 10 × 10 m plot, spaced 1 m apart. We used a laser pointer (designed by Synergy Resource Solutions, Inc. for point intercept sampling in grasslands) to collect data every 0.5 m (2012 protocol) or 1 m (2013 protocol) along each 10 m transect. Analysis of 2012 plot data showed no statistically significant difference between data collected at 0.5 m or 1 m. Thus, we transitioned to data collection at every 1 m in 2013 in order to increase survey efficiency. For each point, we collected data on all layers of vegetation by recording all functional groups (grass, forb, rush/sedge, shrub, and tree) that intercepted the laser point. Nativity, annual/perennial life strategy, and vegetation height (cm) were also recorded, along with a characterization of the soil surface (e.g., soil, rock, litter, woody debris, burrow, or basal intercept of vegetation) at each point. For analysis, a vegetation cover variable was reported as the sum of grass, forb, rush/sedge, and shrub cover (Table 1). Mean shrub cover was less than 10% on all sites except one (13%). Tree cover was less than 1% on all sites and excluded from further analysis. Burrows and surrounding habitat were documented photographically. Lastly, we collected three soil core samples: one at the plot center, and one at both 1 m east and west of plot center.

Soil bulk density was calculated from the volume of the soil corer and soil sample mass. We conducted soil texture analysis using a hydrometer to determine the percent composition of sand, silt, and clay in each sample (Appendix 1). We separated gravel 2 mm or larger from the sample with a sieve, and reported the gravel fraction both as percent of the total sample mass and as a categorical factor (above/below 10% gravel). We then recorded soil texture fractions (sand and clay) as a percent of the soil sample mass (excluding gravel).

2.2. Analysis

We examined each of the habitat variables and their intercorrelations. Univariate logistic regression models were created to identify significant variables. Given the multiple comparisons, we then controlled for the false discovery rate (FDR) using the Benjamini-Hochberg linear step-up method to adjust the p-values (Benjamini and Hochberg, 1995). Significantly correlated variables were then identified using Pearson's correlation coefficients and excluded from regression models together to prevent multicollinearity. Multivariate logistic regression models were used to determine habitat variables associated with squirrel burrow presence and were evaluated using BIC. Chi-square tests were used for categorical data analysis. To aid in model interpretation of the odds ratios, we rescaled the units of the predictor variables and then re-ran models. Site was trialed in modeling as both a random and fixed effect. This was necessary because four sites returned results of squirrels absent or present at all transects. In a mixed effects model, these sites would be confounded by site and excluded, a large loss of data. However, the mixed effect model reports that site accounts for 30% total variance, indicating a need to account for site. The fixed effect model is reported here to include the data from all sites. Analyses were performed on

Table 1
Absolute (not relative) vegetation cover values reported by functional group and total cover. All values are reported as a percentage of the number of points per plot (n = 110). Because plants of differnt types and heights were found at individual points, percent cover can sum to >100%.

Site	Grass (% Cover)		Forb (% Cover)		Shrub (% Cover)		Rush/Sedge (% Cover)		Total Veg (% Cover)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
BT	59	5–87	29	5–65	1	0–8	0	0–0	89	54–114
EL	76	23–99	14	0–38	2	0–37	0	0–0	93	57–105
HW	53	10–128	9	0–36	4	0–15	8	0–58	73	19–129
JM	86	74–98	16	2–36	0	0–5	0	0–0	102	95–110
PO	77	26–96	7	0–41	0	0–0	0	0–0	84	27–117
PD	65	6–98	19	4–45	8	0–31	0	0–0	92	40–131
PG	80	59–100	4	0–15	0	0–0	0	0–0	84	65–107
PR	90	22–100	1	0–5	6	0–46	0	0–0	98	69–105
RA	54	4–120	26	3–51	4	0–34	0	0–0	85	48–135
RP	43	11–81	8	2–15	13	0–32	0	0–0	64	47–85
SY	66	34–89	31	5–62	0	0–0	0	0–0	97	59–124
SN	55	18–80	14	4–52	3	0–34	0	0–0	72	55–88
SW	70	33–100	8	0–31	8	0–45	0	0–0	87	65–100
SC	48	0–87	24	4–48	0	0–6	0	0–0	73	36–97
TH	33	10–75	33	6–87	1	0–9	18	0–57	84	44–139
WH	67	27–99	28	5–65	0	0–1	28	0–84	122	65–176

both the full dataset and the subset of active burrows. Logistic regression was conducted in JMP, version 12.2.0. Generalized linear mixed models (GLMM) were developed in R version 3.2.1 using packages lme4, lmerTest, and AICcmodavg.

Vegetation point intercept data was analyzed as absolute cover values (Table 1). In addition to the field-based soil and vegetation variables, we included 5 fine-scale variables derived from the GIS. For each transect we extracted elevation, slope, and aspect from USGS digital elevation models (10 m precision). Distance to stream and distance to road were calculated from publicly available polygon-based layers (SANDAG, 2015a; b). The distance to stream measure included seasonal streams. California ground squirrels are not dependent on water features, but could derive benefits from proximity to such features. At the landscape scale, we derived soil texture data from NRCS Soil Survey Geographic Database (SSURGO) using USDA Soil Data Viewer version 6.2. Soil texture data was spatially joined to the GPS location of each transect in ArcMap 10.3. We compared field data-based models to equivalent models based on publicly available GIS data layers to indicate relative predictive strength from fine scale and landscape scale data.

3. Results

In 2012, 2013, we collected habitat and soil data at 90 squirrel burrow plots and 138 absence plots across the 16 grassland sites. Recent squirrel activity was confirmed at 71 of the 90 burrow plots.

We modeled site first as a categorical fixed effect (G^2 (15) = 124.85, $p < 0.001$; BIC = 267.92). Grassland-scale grazing or burns could explain some of the variance accounted for by the site variable. The presence of squirrel burrows was found to be 1.7 times more likely where grazing was known to occur (χ^2 (1, n = 208) = 3.60, p = 0.058), as well as 2.6 times more likely where burns had occurred (χ^2 (1, n = 187) = 3.20, p = 0.073), although these findings fell short of statistical significance. The positive relationship between grazing and active squirrel burrows was even stronger (χ^2 (1, n = 191) = 7.07, $p < 0.01$). However, all of these variables are correlated with site and become non-significant ($p > 0.05$) once site is added to the model.

When controlling for site as a fixed effect, the multivariate model that best explained squirrel burrow presence included percent vegetation cover and percent sand (G^2 (17) = 141.37, $p < 0.001$; BIC = 262.24). A 10% increase in vegetation cover was associated with 1.3 fold lower odds of squirrel presence, whereas a 10% increase in percent sand was associated with 2.0 times higher odds of squirrel presence (Table 2). Percent sand was highly negatively correlated with percent silt and clay (*r* (227) = -0.8, $p < 0.001$), so it is likely that a combination of soil texture, not just sand, is driving this relationship.

The univariate adjusted p-values provide confirmation regarding the role of soil characteristics and vegetation cover revealed by the multivariate model (Table 3). Five intercorrelated variables relating to soil characteristics attained significance, indicating that squirrel burrows were more likely to be present when the soil contained more sand, less silt, less clay, less gravel, and higher bulk density. Increasing bulk density is associated with sandy soils. In this region, ground squirrels utilize sandy loam soils with limited clay and gravel fractions. This texture provides soils that are easy to dig in and that maintain the integrity of burrow walls. Vegetation characteristics also appear to be important determinants of squirrel presence, again as reflected in a suite of intercorrelated variables. Squirrel presence was associated with less annual cover, as well as marginally significant trends for less vegetation cover, and less non-native cover. Because annual cover is often composed of non-native species growing in dense monocultures, these three variables are likely measuring the same general preference. For example, non-native and annual cover types were positively correlated with each other (*r* (227) = 0.9; $p < 0.001$) and were negatively associated with squirrel burrow presence. It is thus plausible to conclude that dense, annual non-native vegetation cover deters squirrel presence.

Table 2
Odds ratios and significance values for the selected logistic regression model. Fixed effects are site, percent cover vegetation, and percent sand. The odds ratio reports the odds of squirrel burrow presence versus absence for each 10% change in each variable.

Effects	Units	Odds ratio	95% CI			Reciprocal	95% CI			p
Vegetation cover	10%	0.78	0.65	–	0.92	1.29	1.53	–	1.09	<0.01
Percent Sand	10%	2.04	1.07	–	3.86					0.02

Table 3
Summary of habitat variables for squirrel burrow presence and absence plots. The FDR q-values for each univariate logistic regression model are reported.

Variable	Absence		Presence		Significance
	Mean	SD	Mean	SD	q-values
Soil - % Sand	53.96	13.69	62.62	10.66	<0.001
Soil - % Silt	27.91	8.66	22.78	5.59	<0.001
Soil Bulk Density	0.92	0.18	1.01	0.16	<0.001
Soil - % Gravel	10.02	9.96	5.5	5.26	<0.001
Soil - % Clay	18.13	8.29	14.61	6.84	<0.01
% Annual	88.43	38.16	76.85	25.01	0.04
% Litter	16.52	13.44	20.94	13.55	0.05
% Vegetative Cover	90.8	23.56	83.64	24.52	0.07
% Non-native	83.62	37.52	74.4	26.39	0.10
% Perennial	13.27	27.58	7.64	14.99	0.14
% Soil (Bare Ground)	3.63	6.29	5.56	7.05	0.31
Veg Height (cm)	16.24	9.95	14.39	10.54	0.31
GIS – dist. stream	233.92	195.27	267.07	197.23	0.35
GIS - aspect	114.85	114.49	131.13	122.07	0.46
% Grass	65.3	28.27	62.24	25.87	0.57
GIS – dist. road	309.63	450.76	273.68	373.86	0.69
% Forb	17.83	18	16.64	13.81	0.70
% Shrub	2.69	7.87	3.25	7.91	0.70
GIS - Slope (%)	5.4	6.06	5.18	4.86	0.90
GIS - Elevation (m)	432.62	336.29	436.99	312.57	0.91
% Native	8.48	16.43	8.28	12.99	0.92

When comparing active burrow locations to inactive burrows (sites where burrows were absent were not included in this analysis), percent grass cover and percent litter cover best explained the presence of active burrows (Table 4; G^2 (14) = 30.5, $p < 0.01$). Among the set of sites containing burrows, a 10% increase in grass cover was associated with 2.0 fold lower odds of squirrel presence, whereas a 10% increase in litter was associated with 4.8 fold lower odds of squirrel presence.

In the comparison of field-based models to equivalent models based on GIS data layers, comparable soil texture variables at both scales were available, but gravel and vegetation cover variables were not. However, fitting simple soil texture models was justified since soil texture is invariable and, unlike vegetation cover, usually cannot feasibly be altered with management actions. For a set of two field and two GIS models, 96% of the Aikaike's weight was accounted for by the field-based models (Table 5). The consistent pattern indicates that for soil texture, the fine scale field sampling has greater predictive strength than the landscape scale GIS layers.

4. Discussion

Our study examined a diverse suite of landscape, macro-, and microhabitat factors that might predict the presence of California ground squirrels on the landscape and found that soil texture and vegetation cover (primarily grass and forbs) were the principal factors distinguishing between ground squirrel presence and absence. Surprisingly, although the influence of soil type on burrow construction has been studied previously (Van Vuren and Ordeñana, 2012), it appears that no one has quantified the role of soils in habitat suitability for any North American squirrel. In the subset of sites where squirrels were present, continued squirrel activity and persistence were associated with vegetation conditions (grass and litter cover), and soil texture dropped out of the most predictive model. While soil texture appeared to be influential in the initial occupation of habitat, vegetation cover determined whether squirrels continued to persist and maintain active burrows, consistent with

Table 4
Odds ratios and significance values for the selected logistic regression model including only sites with squirrels present. Fixed effects are site, percent grass cover, and percent litter. The odds ratio reports the odds of recent squirrel activity for each 10% change in each variable.

Effects	Units	Odds ratio	95% CI			Reciprocal	95% CI	p
Grass	10%	0.49	0.26	–	0.93	2.04	1.08–3.86	<0.01
Litter	10%	0.21	0.07	–	0.65	4.78	1.53–14.92	<0.01

Table 5
Model comparison based on AICc and Aikaike weights (AICcWt) derived from a calculation of the relative likelihood of each model. Cumulative weights (CuWt) show which models account for the greatest proportion of likelihood, and k is the number of free parameters in the model. All models are logistic regression models with presence/absence of squirrels as the response variable and site as a random effect.

	Scale	Model	AICc	ΔAIC	AICcWt	CuWt
1	Survey	sand and clay	210.87	0	0.49	0.49
2	Survey	sand only	210.93	0.06	0.47	0.96
3	GIS	sand only	216.85	5.99	0.02	0.99
4	GIS	sand and clay	218.06	7.19	0.01	1

hierarchical multi-scale models of habitat selection (George and Zack, 2001). Plausibly, squirrels settled at sites with suitable soils when vegetation was suitable, but died or abandoned the location when vegetation became less suitable. Alternatively, site abandonment by squirrels may have removed squirrel impacts on vegetation, allowing more dense vegetation to establish.

Our results provide a foundation for implementation of an adaptive management approach (Williams, 2011) in which recovery actions for ground squirrels are used to test factors our analysis has nominated as most important. The data indicate that it may be difficult to (re-) establish ground squirrels in areas where soils are not suitable, namely those with low sand content and high gravel or clay content. In fact, translocated California ground squirrels were less likely to successfully establish in areas where soil had high clay content (Swaisgood et al., 2014). Ground squirrels are most closely associated with friable soils that allow digging for the excavation of burrows. Managers can do little to change soil conditions and therefore site selection is important. However, ground squirrels are associated with more open habitat with less vegetative cover (see also Ordeñana et al., 2012), a variable that managers can influence through various management actions including grazing, burning, mowing or more ambitious (and expensive) native grassland restoration programs (Stromberg et al., 2007).

Our results suggest that non-native vegetation, predominantly grasses, was associated with reduced occupancy by squirrels, although this result did not attain significance. Our data further indicate that the density of vegetation, as measured by percent cover, is more influential than the presence of native plant species per sé. Dense stands of non-native annual grasslands likely impede squirrel antipredator vigilance (sensu Arenz and Leger, 1997). These findings suggest that management activities directed at reducing herbaceous cover will have beneficial effects for ground squirrel establishment and persistence in areas characterized by dense, often non-native grass and forbs. Although vegetation height did not attain significance in our models predicting squirrel presence, we suggest that it is a combination of vegetation density and height that, together, make non-native grasslands less suitable, due to their combined effects on the ability of squirrels to visually detect predators. In fact, ground squirrels translocated to experimentally manipulated non-native grasslands were much more likely to establish burrows where vegetation was shortened by mowing prior to the squirrels' release (Hennessy et al., 2016). However, these vegetation manipulations were not sufficient to encourage translocated squirrel establishment on soils dominated by alluvial deposits characterized by high soil compaction and high clay content which impedes digging (Swaisgood et al., 2014).

These habitat suitability findings will help managers re-establish California ground squirrels and through this management action, may confer other ecosystem benefits. If efforts to locally re-establish ground squirrels near historical densities are successful, these engineers may do more than just help restore functioning ecosystems and assist with conservation-dependent species recovery, but may also help make ecosystems more resilient and stable in the face of climate change (Byers et al., 2006; Allen et al., 2011). Regional scenarios of climate change anticipate temperature and aridity increases along the elevational gradient from the coast to inland (Mastrandrea and Luers, 2012).

Resilience processes provide abiotic functions and feedbacks at strengths influential enough to shift degraded systems into more desired states and, once there, to maintain systems within the desired states (Standish et al., 2014). The abiotic impacts of burrowing (increased soil temperature, nutrient availability, and water infiltration) serve to lower the threshold so that fewer system inputs from humans are required to accomplish the needed shift (Byers et al., 2006). Squirrels also increase the ability of the grassland to maintain its identity under a wide range of conditions (sensu Allen et al., 2011), including conditions of decreased diversity of grass and forb species. At high population densities, squirrels can maintain openings in grass structure through their digging and foraging activities even in areas dominated by non-native annual grass species (Hennessy et al., 2016), while squirrel burrows create habitat for many species in the grassland foodweb (Lenihan, 2007; Schiffman, 2007). Under climate change scenarios, where control over larger-scale processes may not be possible, having an influential engineer at small scales to support resilience and stability may be beneficial.

We agree with Corlett (2015) that active intervention will become increasingly necessary in conservation management and that in Anthropocene landscapes, such as grasslands of the western United States, we need to look beyond returning ecosystems to historical contexts and instead help engineer a brave new future that includes irreversible novel components while minimizing loss of native biodiversity. The Anthropocene provides a different context for management and leads to counterintuitive habitat associations with non-native anthropogenic components of the landscape (Brambilla et al., 2010). In increasingly novel ecosystems, novel components may more often become the target of management (rather than eradication) to increase suitability for target species. In this context, it is as important to understand the basic habitat requirements of keystone species as for species with some degree of rarity. Reliable occurrence records are lacking for the California ground squirrel. As a tool for direct management actions in grasslands, we recommend prioritizing monitoring the presence and distribution of this species. While such intensive programs are not financially or logistically feasible for all wildlife species, it is merited for this neglected ecosystem engineer.

Because much of the potentially suitable habitat for ground squirrels is currently unoccupied due to species eradication and land-use patterns, conservation action should boost squirrel populations at specific locations where they can best serve their ecosystem role and help create and sustain habitat for other grassland species (sensu Delibes-Mateos et al., 2011). Whether managers wish to encourage natural dispersal or actively translocate squirrels, our results help direct these actions by helping managers select areas with suitable soils that could support more rapid population establishment. Less suitable soils may require more ongoing management intervention (e.g., disking, berm creation). An important finding for guiding the selection of suitable management sites is that field-collected data on soils were a much more powerful predictor of squirrel presence than the broad-scale data available from the SSURGO database. Landscape scale datasets of environmental variables are increasingly available through publicly accessible data portals, but an effort should be made to match the scale at which individual species perceive and interact with environmental factors. Managers may therefore use available soil maps to select promising areas for squirrel establishment but are cautioned to include on-the-ground soil testing to ensure soil suitability before investing in restoration efforts. More broadly, these findings remind us to incorporate data collected across multiple scales for better understanding of habitat associations and to improve habitat suitability models used to select restoration and recovery sites.

With regard to vegetation, managers have options. Restoration of native grasslands will certainly be beneficial for squirrels and other native wildlife, but when this is not possible, our data indicate that management of the structure of the grassland habitat will suffice. Managers need to create more open habitat through burning, grazing, mowing, or other methods. Establishing squirrels at high densities may allow squirrels to exert influence over the vegetation structure through their digging and foraging activities and therefore help create a more self-sustaining system requiring less human intervention (Davidson et al., 2012).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.gecco.2018.e00397.

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