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Experimental habitat restoration for conserved species using ecosystem engineers and vegetation management

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Abstract

We experimentally address the theoretical potential for managing ecosystem engineer species to support suites of species in degraded habitats. Historically, the ecosystem engineer California ground squirrel *Otospermophilus beecheyi* supported a grassland food web through widespread burrowing activity. Currently, ground squirrels are not a threatened species, but like many other ecosystem engineers, they exist at densities too low to fulfill their engineering role in many locations. Our objective was to implement short-term treatments, including squirrel translocation, to re-establish key ecological processes on protected reserve lands. We manipulated vegetation and squirrels in a replicated, large-scale field experiment for 2 years, and monitored through a third year. Vegetation mowing and soil decompaction treatments reduced grass density and thatch depth. Squirrel translocation accelerated squirrel settlement and activity in target sites. Of the more than 1000 burrow entrances remaining through the third year, nearly all burrows were concentrated in the plots that received squirrel translocation. We found significant additive effects of squirrel translocation and vegetation management on the spatial footprint of squirrel activity. Noteworthy and persistent engineering effects were achieved through squirrel activity, and both vegetation management and squirrel re-establishment were needed to stimulate squirrel activity. The overarching goal of this experiment was to provide conservation managers with a cost-effective tool for restoring degraded habitats to a hybrid ecosystem state with improved suitability for species of conservation concern, in this case, the western burrowing owl *Athene cunicularia hypugaea*.

Introduction

Habitats are dynamic and the ecological processes that influence those dynamics need to be included in management and restoration plans (George & Zack, 2001). The inclusion of ecosystem engineers – species that modify the environment with consequences for other species and ecosystem processes – may also provide a cost-effective means of achieving conservation targets (Byers *et al.*, 2006). The promise of this approach is twofold: reducing the overall cost by focusing resources on ecosystem engineer reintroduction, and creating the possibility of a more self-sustaining system that is less dependent on continuing human intervention. Here, we provide experimental evidence for the restoration of grassland process through translocation of fossorial (burrowing) ecosystem engineers.

Fossorial mammals are allogenic engineers, in that they modify the existing physical environment rather than creating structure from their own bodies (autogenic engineering) (Jones *et al.*, 2010). A suite of habitat effects (vegetation clipping, burrow construction, and mound-building) are consistently associated with grassland fossorial mammals, from North American prairie dogs *Cynomys* spp., to species such as Patagonian maras *Dolichotis patagonum* in South America, plateau pikas *Ochotona curzoniae* in Asia, and aridland wombat species *Lasiorhinus* spp. in Australia (Davidson, Detling & Brown, 2012). These engineering effects are both distinctive and relatively large compared to strictly abiotic processes operating in grasslands (Reichman & Seabloom, 2002). James & Eldridge (2007) found tantalizing links between reintroduction of engineer species and restoration of key grassland processes with two native Australian burrowing marsupials.

Our specific objective was to test a novel method of supporting populations of western burrowing owls *Athene cunicularia hypugaea*. Most burrowing owl management currently focuses on the installation of artificial burrows, which can habituate owls to artificial conditions in locations that may not otherwise provide appropriate habitat. This raises the possibility of creating ecological traps (*sensu* Battin, 2004), by attracting owls to nest in areas associated with lower fitness due to predation, foraging conditions, or other factors. Although burrowing owl is a widespread species that shows tolerance toward human disturbances and utilizes artificial burrows readily, it is declining across its range (Sheffield, 1997; Desmond, Savidge & Eskridge, 2000; Poulin *et al.*, 2005). In California, burrowing owl population declines are being driven by changes in grassland composition and structure by exotic annual species like wild oat *Avena fatua* and brome *Bromus diandrus* and by reductions in the distribution and abundance of California ground squirrel *Otospermophilus beecheyi*. As an ecosystem engineer, the California ground squirrel both creates burrows and maintains an open vegetation structure beneficial for burrowing owls (Green & Anthony, 1989; Lenihan, 2007). In response, we focused on engineer reintroduction and vegetation management.

Ground squirrels are often found occupying the margins, rather than the interior, of grasslands with mixed native and exotic species composition, suggesting that some component of the habitat is not suitable. Dense exotic ground cover and heavy thatch may reduce the ability of ground squirrels to move, forage, detect predators, and dig burrows. Since reintroductions are more likely to succeed in higher quality habitat (Moorhouse, Gelling & Macdonald, 2009), we hypothesized that habitat modification in the form of vegetation management would be a necessary prerequisite for the establishment of squirrels.

Widespread change to functioning ecosystems has led to the development of hybrid ecosystems incorporating a mixture of historical elements and novel components (Hobbs, Higgs & Harris, 2009). Under this classification, many types of grassland in the western United States can be identified as hybrid. In many locations, the non-native grasses, often of Mediterranean origin, have become the dominant species (D'Antonio *et al.*, 2007). Non-native species can supply functions that benefit native species, such as when they provide foraging opportunities, but the vegetation structure of non-native grasses often differs from the open character of native bunchgrass habitats important for predator detection and avoidance for many native animal species.

Conservation management options for ecosystems may be constrained by the degree of anthropogenic change and difficulty associated with returning the system to historical conditions (Cox & Allen, 2008; Hobbs *et al.*, 2009). Efforts to restore native grasslands have met with mixed success, as changing climate, fire regimes, and other forms of disturbance often favor invasive species (Seabloom *et al.*, 2003*a*, *b*; Cox & Allen, 2008). An alternative approach available to managers is to alter the physical structure of the plant community, by reducing the height and density of non-native grasses. In this way, increased suitability for native wildlife can be achieved through managing non-native species and setting management goals to achieve a hybrid mixture of pre-invasion and post-invasion conditions, rather than trying to undo history.

Our plans, developed with the support of a multi-agency task force, were designed primarily to shift the current, degraded, 'novel' grassland to a hybrid state with some restored native elements of the historical system favorable to fossorial engineers and other native wildlife. Habitat modification to increase suitability for the engineer species, however, does not guarantee engineers will colonize the site. Active management in the form of translocations may be required if resident engineers are not sufficiently close for natural dispersal to take place. Moreover, the rate of colonization may be too slow and cause unacceptable delays in the establishment of desired ecosystem engineering effects. To contend with the difficulties associated with achieving successful translocation (Griffith *et al.*, 1989), we developed translocation protocols that address ecological and behavioral needs of animals relocated to an unfamiliar environment (Shier & Swaisgood, 2012).

Our management actions were implemented in an experimental context so that the contributions of each manipulation could be measured and the lessons learned incorporated into future actions (i.e., adaptive management *sensu* Nichols & Williams, 2006). As the degree of change in physical structure is an important measure of success for management and restoration projects utilizing engineers, our experimental focus was on burrow creation and vegetation structure (Jones *et al.*, 2010). The long-term goal of the broader program is to produce management protocols that can be implemented easily and cost-effectively by conservation managers, and to highlight the relatively unexplored but important role that active management of ecosystem engineers can play in conservation-dependent species recovery.

This study was designed to test (1) whether experimental reductions in vegetation density, thatch depth, and soil compaction support higher squirrel burrowing activity; (2) whether translocating squirrels will produce higher squirrel activity and persistence than vegetation treatment alone; and (3) to examine whether the ecosystem engineering impacts of squirrels include a positive feedback of squirrel activity on vegetation structure through their foraging activities.

Materials and methods

Site description

The study was conducted on two sites in southern San Diego County, which experience a Mediterranean climate of mild, wet winters and hot, dry summers with coastal influence. Rancho Jamul Ecological Reserve consists of former agricultural fields and pasture on sandy loam soils, with plant communities of non-native grasslands dominated by *Avena barbata* and *Bromus diandrus* (full species list provided in Supporting Information Appendix S1), riparian habitat, and coastal sage scrub on upland slopes. The San Diego-Sweetwater National Wildlife Refuge has silt loam soils with cobbles, and a plant community of native (*Stipa pulchra*) and exotic (*A. barbata*, *B. diandrus*, *Festuca perennis)* grassland species and coastal sage scrub. The Jamul site is 10 km inland from and approximately 100 m higher than the Sweetwater site.

Plot establishment

A paired and nested experimental design was utilized to maximize statistical power for detecting treatment effects at a species-appropriate spatial scale. Six sets of paired treatment and control plots were established in grassland sites (Supporting Information Appendix S2). Plots were paired based on similar vegetation community, soil type, slope, aspect, and proximity. Each circular plot was 100 m in diameter, with an area of 7854 m^2 (0.79 ha). The plots within each pair were separated by at least 50 m, and pairs were separated by a minimum of 300 m. The female California ground squirrels occupy a home range of approximately 600–900 m^2, or a radius of 14–17 m around the burrow with extensive overlap of individual home ranges (Boellstorff & Owings, 1995). Each plot was divided into three equal wedge-shaped subplots. The subplots received one of three treatments: control, mowing, and mowing plus soil augering. Squirrels were translocated into one plot from each pair (Fig. 1). Four pairs of plots were established in 2011 (RJER1-3, SWTR), and two pairs of plots were established in 2012 (RJER4, RJER5).

Vegetation and soil treatments

Mowing was conducted without heavy motorized equipment to minimize soil compaction and extensive surface disturbance. Vegetation treatments were conducted for two consecutive years in May, at the end of the growing season for annual grasses but before the grasses had dried out. Vegetation was mowed to a height of 7.5–15 cm using handheld string trimmers, and the resulting thatch was raked and removed. There was no evidence of soil disturbance from mowing or thatch removal.

Soil decompaction was implemented by augering 20 holes per subplot to produce a density of one hole every 10 m^2. Holes were drilled to ~0.3 m depth on a 45° angle with a one-person handheld auger fitted with a 15 cm auger bit.

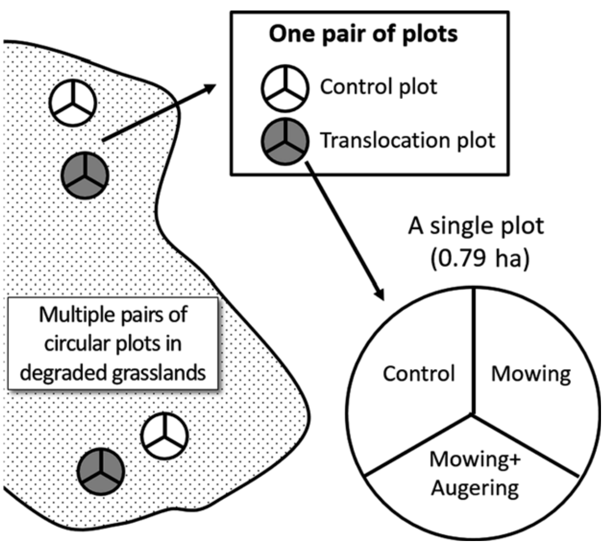

Figure 1 Paired design of the habitat enhancement/squirrel translocation experiment.

Squirrel translocation procedures

California ground squirrels were captured for relocation from source sites 3–16 km from the release site, with a target number of 30–50 squirrels translocated to each plot (minimum of three adult males and six adult females, plus weaned pups). An attempt was made to maintain familiar social groups of individuals. Squirrels live in colonies of a few dozen individuals, in overlapping territories, and exhibit year to year site fidelity (Boellstorff & Owings, 1995). After a short holding period, squirrels were transferred to acclimation burrows with above- and below-ground protection, and provided with water and food. After 1 week, acclimation cages were removed, and squirrels were released.

A second year of translocations was conducted to supplement the initial squirrel populations. The supplemental translocations occurred in August (in contrast to the June timing of the initial translocations). In the second year, debris piles were also added to the plots to provide additional cover as a refuge from predators.

Assessment methods

In all plots, vegetation structure and species cover were measured prior to the first treatment. Post-treatment assessments were conducted after both the vegetation and squirrel translocation treatments had occurred. Pre- and post-treatment assessments were also conducted in the second treatment year, and spring and fall assessments were conducted thereafter.

Vertical vegetation density was assessed, using a Robel pole vertical obstruction method, to a height of 1 m (Herrick *et al.*, 2005). Vertical vegetation density measures habitat structure in terms of height and density of vegetation cover. Vegetation density is expressed as a percentage of the vertical column occupied by vegetation from the ground level to 1 m. The Robel pole was placed at three points along each transect (at 5, 12, and 19 m). Two measurements were read at each position from a distance of 5 m.

Observers walked a grid pattern through each subplot and recorded California ground squirrel activity. Burrows with an opening of at least 7 cm at the point of maximum diameter were recorded as probable California ground squirrel burrows (Lenihan, 2007). The size and shape of both the burrow entrance and the burrow apron (the disturbed area around the burrow cleared of all vegetation) were recorded.

Statistical analysis

Mixed effects modeling was used to analyze treatment effects on vegetation structure and ground surface disturbance

(Gelman & Hill, 2007). For vegetation structure, the calculation of vertical vegetation density is described above, and was modeled with the identity of the matched pair of experimental plots (pair ID) and a split plot effect (vegetation treatment nested within pair) as random effects. Pair ID accounted for pair-level variance due to both site and the year the pair was initiated. The time point (number of years into the experiment: year 1, year 2, year 3) was modeled as a fixed effect.

A sequential analysis of squirrel activity was conducted. The first model was a logistic mixed effects regression for the effect of squirrel translocation (n = 96) on squirrel activity (presence/absence), with squirrel translocation (control, translocation) and number of years into the experiment as fixed effects, and pair ID as a random effect. Due to the many zero values in translocation control plots, a second mixed effect regression was then modeled for the effect of vegetation treatment on squirrel activity for squirrel translocation plots only. To create a response variable representing a measure of overall ground surface disturbance per subplot, the apron areas measured at each burrow were summed by subplot. A log (n + 1) transformation was applied due to right (positive) skew resulting from the few established, occupied burrow complexes with larger entrances and apron areas compared to the many small 'starter burrows' that had small entrances and aprons. The fixed effect factors were vegetation treatment (control, mow, mow/auger) and number of years into the experiment. The random effect factors were pair ID and the split plot effect (vegetation treatment nested within pair).

The burrow counts from spring of year 3 were also modeled with Poisson mixed effects regression. The fixed effects were vegetation treatment and squirrel translocation, and the random effect was vegetation treatment nested within pair ID.

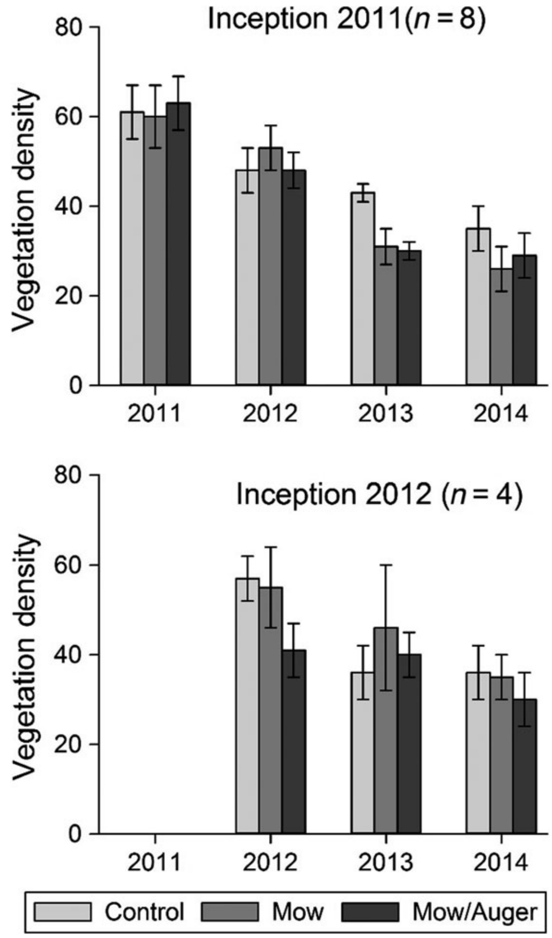

Figure 2 Vertical vegetation density measured April 2011–2014, grouped by year of plot inception. Vegetation density is expressed as a percentage of the vertical column from ground level to 1 m. In the first 2 years after plot initiation, vertical density was measured before annual vegetation treatments.

Results

Vegetation structure

Mixed effects modeling indicated no significant treatment effects on vertical vegetation density (Fig. 2). In contrast, the main effect of year was associated with annual reductions in vegetation density during an ongoing drought ($F_{3,108}$ = 31.62, $P < 0.001$). Decreased growth due to drought may have influenced relatively small vegetation treatment effect sizes (Fig. 2).

Squirrel burrowing activity

Throughout the experiment, the overall footprint of squirrel activity on the plots continued to increase, and squirrel activity was concentrated in the plots that received squirrel translocation ($P < 0.001$). In year 3, 974 of 1028 (94.7%) burrows were found on the plots that received translocated squirrels (Fig. 3). The pattern of burrows in control plots was weak and patchy.

The counts of squirrel burrows were higher in the mow/auger subplots than the control ($P < 0.001$), and marginally higher in the mow-only subplots ($P < 0.1$). For year 3 data, the proportions of burrows in the mowing only subplot ranged between 16% and 50% (mean = 33%) and in the mow/auger subplots between 27% and 62% (mean = 47%); by contrast only 5% of burrows were found in all treatment subplots of the plots without translocation (Fig. 3). Repeated sampling through time showed that these proportions were stable, indicating that the initial burrowing sets the pattern for years to come. Once a burrow is established, the squirrels continue digging in the immediate vicinity, creating a burrow complex.

Analysis of the apron area of disturbed ground surrounding squirrel burrows also shows substantive effects of squirrel and vegetation treatments, as well as time effects (Tables 1, 2). Ground disturbance increased across time points from year 1 to year 3 (Table 2). Overall ground disturbance was highest in squirrel translocation subplots that received both mowing and augering (Fig. 4). The vegetation and squirrel translocation effects are additive, indicating that both mowing and squirrel translocation are needed to achieve

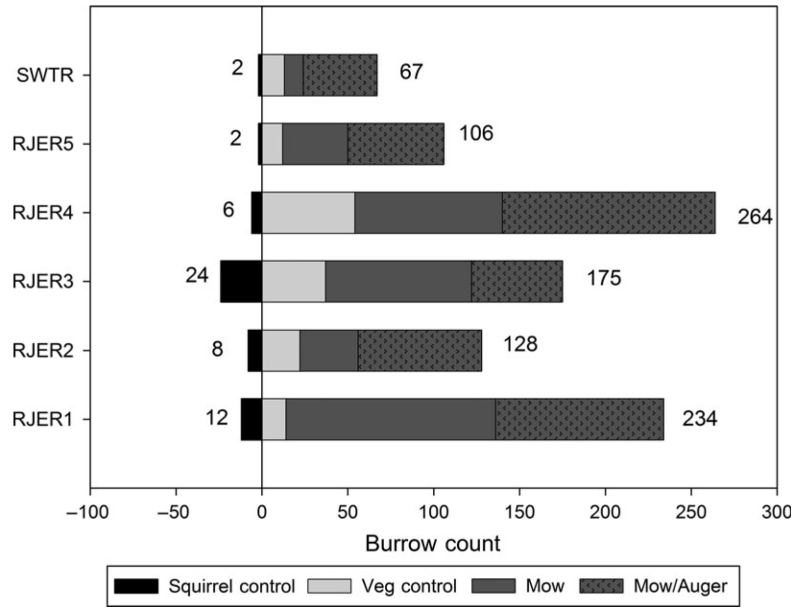

Figure 3 Burrow counts from spring of year 3 for each of the paired squirrel translocation plots.

Table 1 Logistic mixed effect regression for the effect of squirrel translocation ($n = 96$) on binomial squirrel activity (presence/absence), with squirrel translocation and time point as fixed effects and plot pair ID as a random effect

Fixed effect	Level	Log odds	95% CI	*P* value
Intercept		−0.77	−2.55 to 1.03	0.31
Translocation	Control	0		
	Translocate	3.9	2.32 to 6.11	<0.01
Time point	Year 1	0		
	Year 2	1.25	−0.15 to 2.80	0.09
	Year 3	1.43	−0.22 to 3.32	0.11

The analysis includes post-treatment data from years 1–2 and year 3 fall monitoring.

Table 2 Linear mixed effects model results from burrowing activity, measured as apron area, sampled during 2011–2014 ($n = 46$)

Fixed effect	Level	Estimate	95% CI	*P* value
Vegetation	Control	0		
Treatment	Mow	49.1	5.2–405.4	0.01
	Mow/Auger	212.8	36.4–1287.3	<0.01
Time point	Year 1	0		
	Year 2	8.3	3.7–18.1	<0.01
	Year 3	28.5	12.6–63.6	<0.01

Squirrel translocation control plots have been excluded. The data were log ($n + 1$) transformed, and the coefficients have been back-transformed (units in m^2). The analysis includes post-treatment data from years 1–2 and year 3 fall monitoring. Random effects accounted for 69% of total variance.

high levels of squirrel burrowing activity. Both response variables suggested higher activity with the augering treatment, although this effect was variable by plot.

Discussion

Given the mounting evidence showing that the California ground squirrels (and other burrowing animals elsewhere) play a key role in engineering grassland ecosystems (Reichman & Seabloom, 2002; James & Eldridge, 2007; Davidson *et al.*, 2012), it is surprising how little attention this species has received in conservation planning and policy. Squirrels were historically, and still are widely perceived as pests that damage crops and need to be controlled (Marsh, 1998). Squirrels have been targeted by control efforts and have been eradicated in many locations (Lenihan, 2007). Continuing eradication efforts keep ground squirrels at 10–20% of historic population levels (Marsh, 1998). While it may not be possible to increase ground squirrel activity at large scales, it is realistic to return them to targeted, protected reserve lands as a key component of restoring more functional grasslands. The experiment was based in a grassland ecosystem, but the engineering implications transfer across ecosystems, including the potential for recognizing and utilizing the engineering effects of species treated as pests (Delibes-Mateos *et al.*, 2011).

Effects of experimental vegetation management and squirrel translocation on ecosystem engineering

Our results indicate that the best management approach will often require both vegetation management and squirrel

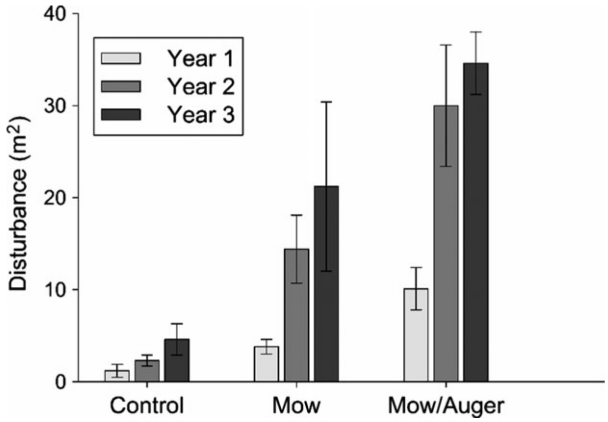

Figure 4 Overall ground surface disturbance (derived from the apron areas measured at each burrow) as a proxy for squirrel activity during 2011–2014 ($n = 6$). Only plots treated with squirrel translocation are included, since ground disturbance on the non-translocation plots was effectively zero.

translocation, as the combination supports higher levels of squirrel activity than the use of either strategy alone. In terms of mowing treatment effects, although the effects of vegetation reduction were less persistent than hoped, the treatment provided an immediate benefit to squirrels, as evidenced by rapid movement of released squirrels from unmowed control subplots to mowed areas. The experimental mowing also had significant effects on squirrel activity. Within the squirrel release plots, mowed subplots had large numbers of burrows, whereas few squirrel burrows were located in the unmowed control subplots. Apparently, the conditions produced by mowing encouraged squirrels to colonize treated areas. The lack of squirrel activity in matched-control plots indicates that in areas without large nearby squirrel populations, vegetation treatment alone will not encourage rapid colonization by squirrels.

Reintroduction of an ecosystem engineer

An important outcome of this project was the finding that squirrel translocation can successfully create more numerous burrow complexes than artificial burrow installations. Our translocated squirrels created nearly 1000 burrows, an achievement that would be difficult and expensive to replicate with artificial burrows. Artificial burrows, with their simple configurations of one or two entrances and one chamber, cannot match the complexity of natural burrows, and also have the added expense of human maintenance costs in perpetuity (VanVuren & Ordenana, 2012). Moreover, patterns of burrow usage by breeding owls indicates that a family of owls needs multiple burrows in the vicinity, as chicks are moved between several burrows, and fledglings disperse to burrows in the vicinity of the natal burrow before they initiate end-of-season migration (Davies & Restani, 2006).

There are other reasons to broaden the focus of management to include fossorial mammal interactions. The decline of fossorial mammals has been implicated as a key factor in declining burrowing owl populations in the Great Plains of the United States (Kotliar *et al.*, 1999; Desmond *et al.*, 2000; Smith & Lomolino, 2004), Argentina (Machicote, Branch & Villarreal, 2004) and southern California (Lincer & Bloom, 2003). In addition to the benefits of burrow creation, owls benefit from a suite of indirect interactions with fossorial mammals, including effects on prey availability (Lenihan, 2007). The presence of ground squirrels likely also provides some protection from predators, because ground squirrels spend significant energy on vigilance, and squirrels and owls share many of the same predators. Ground squirrels use antipredator vocalizations and visual displays to maintain an early warning system for predator detection and deterrence (Owings & Hennessy, 1984; Loughry & McDonough, 1988; Swaisgood, Owings & Rowe, 1999) and owls may benefit from ‘eavesdropping’ on these signals. Such heterospecific eavesdropping is not uncommon and confers important fitness benefits (Schmidt, Dall & van Gils, 2010). Antipredator calls may aid in predator evasion and periods with no alarm calls may signal safety, enabling eavesdroppers to focus on foraging instead of vigilance. Burrowing owls living in association with black-tailed prairie dogs appear to benefit from these effects, as they experience lower predation levels (Desmond *et al.*, 2000). Thus, squirrels and other fossorial mammals have important benefits for burrowing owls beyond the provision of burrows for nesting.

The presence of squirrels also supports a wider community. Squirrel burrows are utilized by many reptiles, rabbits, and invertebrates such as tarantulas and burrow-specialist beetles (Schiffman, 2007). Sites with ground squirrel colonies have quantitatively greater diversity levels of reptiles, amphibians, insects and birds than sites where squirrels are absent (Lenihan, 2007). There is ample historical evidence that digging and foraging disturbances by ground squirrels have physical effects on soil structure, temperature, nutrient levels, and vegetation composition patterns (Schiffman, 2007). These interactions suggest that California ground squirrels should be considered an ecosystem engineer in California grasslands (Byers *et al.*, 2006; Gutierrez & Jones, 2006). At a minimum, ground squirrels are a key species in these ecosystems.

Squirrel effects on vegetation structure

As the effects of structural change can feed back on future engineering activity levels, we examined the strength of squirrel effects on vegetation structure (Jones *et al.*, 2010). Squirrels cut and trample grass and forb stems during their normal foraging activity, and qualitative observations of a lower and more open vegetation community with squirrel activity have been published (Evans & Holdenried, 1943; Fitch, 1948; Lenihan, 2007). For owls, low vegetation makes detection of predators and prey easier and they appear to have a preference for this vegetation structure (Green & Anthony, 1989; Clayton & Schmutz, 1999). The extensive spatial extent of communities dominated by tall and dense exotic annual grass and forb species increases the importance of the effect of squirrel activity on vegetation structure.

We hypothesized that if squirrel density were sufficiently high in the vegetation treatment subplots, their foraging activities would sustain the effects of the mowing treatment, helping to maintain a more open habitat structure. Our transects were designed to capture large-scale plot-level effects, but we detected no effect of squirrels on vegetation structure at this scale. However, squirrels had obvious effects at smaller spatial scales on vegetation in the immediate vicinity of the burrow, creating open ground and thinned grass cover around burrows from digging and foraging activities. These effects appeared to increase with time after the burrow was established. Our current assessment is that squirrels do have a substantive impact on the microhabitat around burrows and that with time a squirrel colony at historical densities may have larger, plot-level impacts on vegetation structure.

Conservation and management

The experimental design allowed us to test various management alternatives against one another (e.g., translocating squirrels vs. natural squirrel colonization and different forms of habitat management). The results indicate clear lessons learned, and inform both future management actions and future research questions to further refine management protocols. We anticipate that the primary usage of this management protocol will be the creation of burrow nesting habitat for burrowing owls on targeted protected sites.

The theoretical best-case scenario of an intrinsically self-sustaining ecosystem after reintroduction of the ecosystem engineer (Byers *et al.*, 2006) was not realistic due to established exotic seed banks at all of our sites. Therefore, we set a modified goal that reintroduction of the ecosystem engineer would shift the site to a more sustainable hybrid state (Hobbs *et al.*, 2009). It is now evident that a realistic hybrid state would consist of dominant exotic grass cover, active human management of grass structure, burrowing activity by squirrels, and breeding owls. The potential stability of this hybrid ecosystem is uncertain but will be influenced by abiotic and biotic indirect effects of the ecosystem engineer (Byers *et al.*, 2006).

Managers might best leverage the findings of this experiment by identifying target sites where owl occupancy is desired, and where either component of vegetation management and squirrel presence is already in place. Our results show that active squirrel translocation was needed at the sites where we worked, but different starting conditions regarding the proximity and abundance of squirrel populations may be more conducive to natural squirrel colonization provided vegetation management creates favorable habitat. Adding vegetation management to a site with a small population of resident squirrels may increase the size of the colony and squirrel activity levels. Future work can test this hypothesis and explore the potential for this more cost-effective solution to ecosystem engineer recruitment in some prescribed circumstances.

Our results indicate that ongoing vegetation management is likely required to retain a more open habitat structure, but alternatives to mowing, for example grazing and fire, may be evaluated with regard to efficacy for squirrel establishment. Our study also did not rule out an ecosystem engineering role for squirrels on vegetation management. Future work could explore whether larger number of squirrels established for longer periods of time help maintain more open habitat or alter the competitive balance in the plant community in favor of native grasses and forbs. The long-term goal of re-establishing burrowing owls to these restored habitats is the next and most important goal to validate our approach.

Our approach carries broad implications for management of conservation-dependent species across geographic regions and contexts. The new 'anthropocene' era in which we currently live demands bold conservation interventions to maintain species and habitats (Corlett, 2015). It is important that solutions contain re-establishment of ecological processes required for the recovery of target species. The use of ecosystem engineers may be a more reliable tool for achieving these conditions in more sustainable ways. A call for better scientific understanding of ecosystem engineers is warranted, and experimental approaches to restore engineer species and measure their effects on conservation outcomes play a key role in that endeavor.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Full species list by functional group (forb/grass/shrub), taxonomic family, and nativity.
Appendix S2. Final plot locations (UTM coordinates reported in projected coordinate system NAD1983 Zone 11N).