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Restoration of Native Plants Is Reduced by Rodent-Caused Soil Disturbance and Seed Removal☆,☆☆

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A B S T R A C T

Granivory and soil disturbance are two modes by which burrowing rodents may limit the success of native plant restoration in rangelands. This guild of animals has prolific effects on plant community composition and structure, yet surprisingly little research has quantified the impact of rodents on plant restoration efforts. In this study, we examined the effects of seed removal and soil disturbance by the giant kangaroo rat *(Dipodomys ingens)* on native plant restoration in a California rangeland. Using experimental exclosures and stratifying restoration plots on and off rodent-disturbed soil, we assessed the individual and combined effects of seed removal and soil disturbance on seedling establishment of four native plant species. Across all species, biotic soil disturbance by kangaroo rats reduced seedling establishment by 19.5% (range = 1–43%), whereas seed removal reduced seedling establishment by only 6.7% (range = 4–12%). Rates of seed removal across species weakly paralleled kangaroo rat dietary preferences. These results indicate the indirect effects of burrowing rodents such as kangaroo rats on native seedling establishment via changes in soil properties may rival or exceed the direct effects of seed removal.

Introduction

Native grasslands are among the most critically endangered ecosystems in the United States (Noss et al., 1995), making native grassland restoration a priority for many conservation land managers. However, grassland restoration success has been limited by a lack of knowledge about the factors that affect restoration outcomes and how these factors can be manipulated to improve success (Aronson, 2013). Rodents are common in grassland ecosystems, and disturbance by rodent populations may therefore be an important factor affecting restoration success.

As burrowers, herbivores, and granivores, small mammals can have considerable effects on plant community composition and structure (e.g., Brown and Heske, 1990; Schiffman, 1994; Brock and Kelt, 2004). In extreme cases, rodents can remove up to 90% of local annual seed production (Chew and Chew, 1970; Soholt, 1973), clear vegetation from up to 32% of the landscape (Schiffman, 1994), and turn over the entire soil surface every 3 to 15 years (Hobbs and Mooney, 1995). Researchers and restoration practitioners have acknowledged that rodents may strongly impact restoration projects (e.g., Longland and Bateman, 1998; Watts, 2010; Longland and Ostoja, 2013). However, relatively few studies have examined the mechanisms by which rodents affect plant restoration, and these studies have focused primarily on the effects of granivory (e.g., Hoffmann et al., 1995; Orrock et al., 2009; Orrock and Witter, 2010). The effects of other rodent interactions (e.g., biotic soil disturbance) on restoration success remain largely unknown.

Rodent-disturbed microsites often have soil characteristics that differ markedly from less disturbed areas just meters away (Grinnell, 1923). As central place foragers, burrowing rodents tend to concentrate nutrients and organic matter from larger areas into smaller areas (Mun and Whitford, 1990). Rodents can also transport material vertically through the soil profile surface (Whitford and Kay, 1999). Collectively, these actions can cause significant changes in a variety of soil properties including bulk density, soil temperature, infiltration, soil moisture, pH, and soil nutrient levels (Whitford and Kay, 1999). These indirect effects of rodents on soil properties have been proposed as possible mechanisms explaining the keystone effects of kangaroo rats (Brown and Heske, 1990; Guo, 1996).

Rodent burrowing may be particularly important in nonequilibrium systems such as arid and semiarid rangelands, where productivity is moisture limited and there is a positive relationship between aridity and interannual variability of rainfall (Sullivan and Rohde, 2002). In nonequilibrium systems, theory suggests that abiotic factors such as soil properties, site characteristics, and weather generally have more influence on plant community structure than direct biotic interactions

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such as herbivory and granivory (Jackson and Bartolome, 2002). Consequently, a number of recent restoration studies have focused on the effects of abiotic variables such as site preparation techniques or soil amendments (e.g., Bonebrake et al., 2011; Doll et al., 2011; Kulmatiski, 2011). Rodent-caused changes in the physical and chemical properties of soil could function similarly to soil amendments, by acting as ecological filters that favor the assembly of certain species over others, independent of rodent seed preferences and seed removal.

In California's Carrizo Plain, *Dipodomys ingens* (giant kangaroo rat, hereafter GKR) dominates the rodent community and is thought to be a "keystone species" and "ecosystem engineer," as it has a disproportionately large impact on the grassland community and physically transforms the landscape (Prugh and Brashares, 2012a). Like other kangaroo rats, GKRs are primarily seed eaters (granivores) and consume vast amounts of both native and exotic plant seeds (Shaw, 1934; Williams et al., 1993). GKRs typically cut the ripening seed heads of grasses and forbs and sun-dry the seeds in either buried pit caches or in stacks on the soil surface (Shaw, 1934; Williams et al., 1993). GKRs later relocate buried caches and transfer the contents into long-term storage chambers in their burrow mounds (Shaw, 1934; Williams et al., 1993). GKR burrow mounds are established over many generations, and long-term occupancy results in mima-mound topography (Williams and Kilburn, 1991; Fig. 1).

Here, we sought to identify the individual effects of GKR seed removal and soil modification on the success of rangeland restoration efforts. We first assessed GKR seed preferences using cafeteria-style diet trials. We then quantified and compared the effects of seed removal, biotic soil disturbance, and soil chemistry on the seedling recruitment of four native plant species selected from our diet trials. These four species were selected to include a variety of growth forms and span a range of GKR seed preferences. Using experimental exclosures, we established small-scale restoration plots in areas that were accessible and inaccessible to kangaroo rats and stratified plot locations on and off GKR burrow mounds.

Methods

Study Area

We conducted this study from 2008-2011 in a semiarid annual rangeland within the Carrizo Plain National Monument, in southeastern San Luis Obispo County, California (Fig. 2). This study was a component of a larger long-term study initiated in 2007 to experimentally examine interactions among cattle, plants, and wildlife in the Carrizo Plain (Prugh and Brashares, 2012b). Parts of the monument were grazed by sheep and cattle when vegetation levels exceeded thresholds (U.S. Bureau of Land Management, 2010). The Carrizo Plain is the largest contiguous grassland in California, and it is among the last refuges for many species endemic to the San Joaquin Valley ecoregion (Germano et al., 2011). Precipitation in the Carrizo Plain is highly variable (annual CV = 47%), averages 209 mm per year, and falls primarily as rain during the winter months (MesoWest, 2011). Rainfall was nearly 50% above average when restoration plots were established, totaling 302 mm in the 2010 water year (MesoWest, 2011). The above-average rainfall likely resulted in better growing conditions and improved seedling establishment rates relative to normal conditions for some plants. Perennial bunchgrasses, most notably *Poa secunda* (Sandberg's bluegrass), may have once dominated the southern San Joaquin Valley region alongside native annual forbs (Germano et al., 2001). Exotic annual species including *Bromus madritensis ssp. rubens* (red brome), *Erodium cicutarium* (red-stem filaree), and *Hordeum murinum* (foxtail barley) are now abundant in the Carrizo Plain, and native plant cover has declined (Schiffman, 1994; Germano et al., 2001).

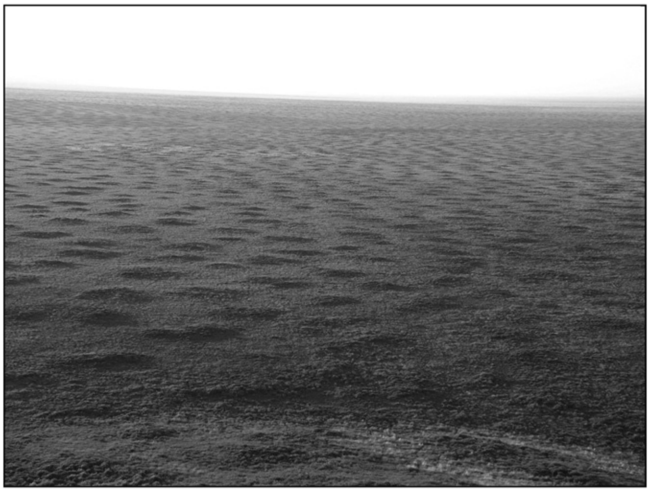

Fig. 1. Mima-mound topography that dominates the landscape in the study area within the Carrizo Plain National Monument, California. Photo credit: Don Johnson.

Our study area was located within the core habitat of the GKR, on flat terrain with no shrub cover (Fig. 2). The GKR is a state and federally listed endangered species that has experienced severe habitat loss but is locally abundant within the Carrizo Plain (Williams and Kilburn, 1991). The GKR is the most abundant member of the rodent guild in the Carrizo Plain and was the only primarily granivorous rodent species present in our study area (Prugh and Brashares, 2012a). Extensive trapping of GKR was conducted twice annually on our study sites beginning in 2007. From 2007–2012, average densities of GKR never fell below 25 ha^{-1} and peaked at more than 50 ha^{-1} (Prugh and Brashares, 2012b). GKR burrow mounds covered roughly 20% of the landscape (Bean et al., 2012). The high densities of GKR observed within the study area are fairly typical during years without extended droughts (Williams et al., 1993).

Diet Trials

We conducted cafeteria-style diet trials to assess the dietary preferences of GKRs. We collected ripe seed heads of the 12 most common plant species found on our plots in April 2008. We randomly chose 30 GKR mounds spread throughout our study area for diet trials, which were conducted 14 July 2008 to 28 July 2008. On each selected mound, we dug a shallow trench (approximately 1 m long, 6 cm wide, and 1 cm deep) and placed 0.5 g of seeds from each of the 12 plant species in separate piles along the trench. The order of species along the trench was randomized in each trial. We returned at dawn the next day to collect and weigh remaining seeds. Motion-trigger cameras were used to ensure GKRs visited each trench. Additionally, controls with wire mesh cages that were accessible to ants but not GKRs were initially used to assess whether seeds were being removed by ants. These controls resulted in only negligible amounts of seed removal (mean of 3% removal). For each trial, selection ratios (SR) were calculated as the proportion of each species removed relative to proportions available:

$$SR = \frac{U_i}{P_i * \sum U_i} \qquad (1)$$

Where U_i = weight of seeds of species i removed and P_i = proportion of available seed (based on weight) composed of species i (Manly et al., 2002). Selection ratios > 1 indicated preference and ratios < 1 indicated avoidance. Mean selection ratios for each species were calculated across the 30 trials, along with standard errors and confidence intervals. Results of diet trials were used to select plant species for seeding in restoration plots.

Experimental Design

To examine effects of seed removal and soil disturbance on native seeding efforts, we used a randomized split-plot experimental design with two factorial treatments: kangaroo rat presence and burrow presence. In 2007, stratified randomization was used to place 10 experimental

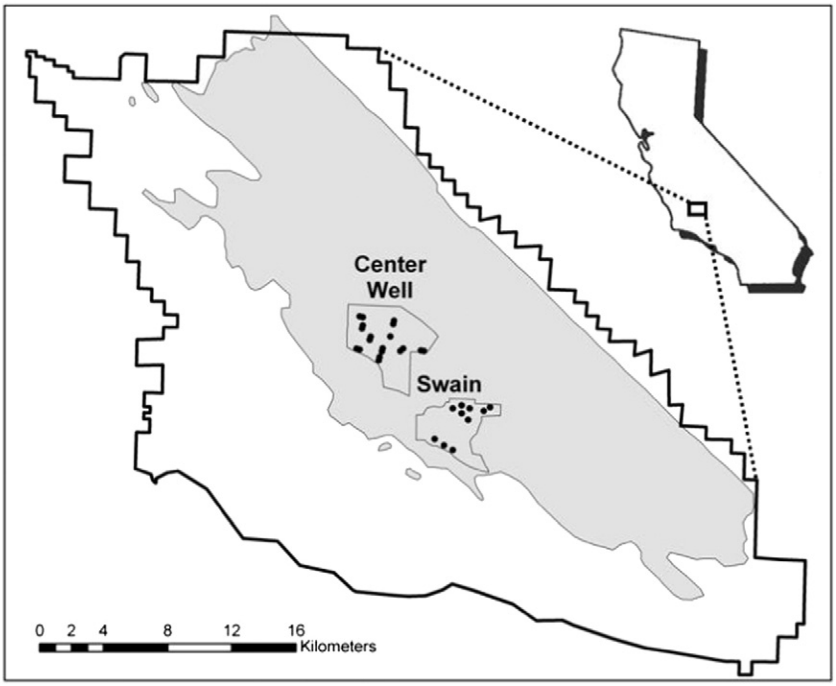

Fig. 2. The Carrizo Plain National Monument, California (39º15′N, 119º50′W), showing the current distribution of the giant kangaroo rat *(Dipodomys ingens)* in gray and experimental sites in the Center Well and Swain study pastures.

sites within each of two large pastures in the core range of the GKR ($n =$ 20 sites total). All sites were separated by at least 0.5 km (Fig. 2). The Swain pasture (6 570 ha) had abundant perennial bunchgrasses, was dominated by sandy loam soils, and had well-developed burrow mounds. The Center Well pasture (16 300 ha) had almost no perennial cover, was dominated by loam soils, and had less developed burrow mounds.

A 20 × 20-m kangaroo rat exclosure was constructed in the center of each experimental site, and a paired sampling area (also 20 × 20-m) was located in a random compass direction 20 m from each exclosure. Exclosures were constructed from 1-cm mesh hardware cloth and secured with rebar and T-posts. Hardware cloth extended 0.6 m below ground (to prevent GKRs from burrowing under) and 0.91 m above ground, with a 0.15 m overhang at the top of the exclosures (to prevent GKRs from climbing over). Resident kangaroo rats were removed from rodent exclosures by live-trapping and released outside of the treatment and control areas in artificial burrows. Rodent exclosures were checked monthly for signs of rodent activity, and any GKRs present were live-trapped and relocated (approximately 1–10 breaches occurred per year across the 20 exclosures).

Approximately half of each 400-m^2 sampling area consisted of GKR burrow mounds, which were 7 to 10 m in diameter. Although the locations of burrows could not be controlled experimentally, GKRs are highly territorial (Cooper and Randall, 2007), and the remarkably regular spacing of burrows (Fig. 1) indicated that burrow location was determined by territoriality rather than microsite differences. GKR presence was therefore a whole-plot factor and burrow presence was a subplot factor, each with two treatment levels (present/absent, burrow/nonburrow). At 19 of the 20 experimental sites, four 1-m^2 restoration plots were established from 11 January 2010 to 16 January 2010. One site in the Swain pasture was excluded from restoration treatments because existing cover of *Poa secunda* was dense enough that excessive disturbance would have been required to prepare the plots for our seeding trials. Two plots were located within each 400 m^2 rodent exclosure, and two were located within the paired sampling area accessible to GKRs (Fig. 3). In each 400 m^2 sampling area, plot locations were randomly selected and stratified by burrow mounds such that one plot was located on a burrow mound and one was located in the undisturbed intermound space (all plots were located > 2 m from the fence line; Fig. 3). Thus the factorial treatment combinations were: (1) "GKR + Burrow Mound," (2) "GKR + Intermound," (3) "No GKR + Burrow Mound," and (4) "No GKR + Intermound," with one restoration plot per treatment combination per site (total $n = 76$ plots).

Site Preparation and Seeding

Sites were prepared and seeded from 11 January 2010 to 16 January 2010. Because burrow mounds were inactive within the rodent exclosures, soil on the burrow mound plots inside the exclosures was artificially disturbed immediately before seeding. On each plot, two tunnels were made using a 7.5-cm soil corer, each running 15 to 30 cm below ground under the plots, and the loose soil removed from the corer was placed on the plot surface. This simulated rodent disturbance in two ways: (1) by lowering the soil bulk density on the surface and (2) by bringing soil from depth, with differing chemical composition to the surface. Similar methods have been used successfully to simulate gopher disturbance (Kotanen, 1997; Laundré, 1998).

All plots were prepared by hand-weeding before seeding, while inactive burrow mound plots within exclosures also received artificial soil disturbance as described earlier. Four trenches were made on each plot, each 1-m long and 1-cm deep. Trenches were parallel to each other and separated by 20 cm. One of four native plant species (Table 1) was randomly assigned to each of the four trenches on each plot, and 0.5 g of locally collected seed was distributed evenly throughout the trench and covered in soil. These conditions, including seeding depth (1 cm) and seeding density (2.0 g · m^{-2}), were consistent with recommendations for drill-seeding (Stromberg et al., 2007) and simulated commonly used restoration practices. The four native plant species seeded were *Calandrinia ciliata* (red maids), *Lepidium nitidum* (peppergrass), *Poa secunda*, and *Festuca microstachys* (small fescue). These species were selected because they represented a variety of growth forms and spanned a range of preference by GKR in our diet trials (Table 1).

Seedling Establishment

From 21 March 2010 to 25 March 2010, seedling establishment was measured using the frequency sampling method. Frequency sampling is commonly used in rangeland monitoring and represents a combination of

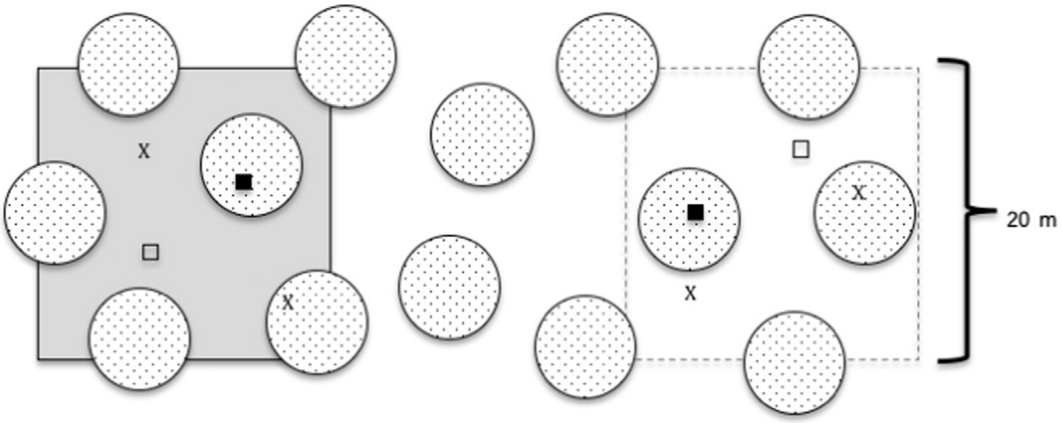

Fig. 3. An example experimental site in the Carrizo Plain National Monument, California. The gray box with the solid line represents a giant kangaroo rat exclosure, and the white box with the dashed line represents a control sampling area accessible to kangaroo rats. The dotted shapes show burrow mounds. Soil sample locations are marked with an "X," and restoration plots are indicated with filled (burrow mound) and open (intermound) boxes.

species attributes including density, dispersion, and cover (Despain et al., 1991). This method is particularly useful when it is difficult to separate and count individuals, as is often the case for grass seedlings. Ten 10 × 10-cm quadrats were positioned in a row over each seeded trench, and the presence/absence of live seedlings of the target species within each quadrat was recorded. Frequency counts therefore ranged from 0 to 10.

Soil Characteristics

To assess the effect of GKR presence and burrowing on soil properties, 80 soil samples were collected in August 2011. Cores were 5 cm in diameter and 15 cm deep, and samples were homogenized before analyses. Similar to the restoration plots, a total of four samples were taken at each experimental site (Fig. 3). In each sampling area (exclosure and control), one soil sample was taken from a random location on a GKR burrow mound and one was taken from a random location in the intermound area. Soil samples were analyzed for bulk density according to recommended guidelines (Robertson et al., 1999) and were sent to the Analytical Laboratory at University of California, Davis (http://anlab.ucdavis.edu/analyses/soil) for a soil fertility panel analysis. See Table 2 for the soil properties analyzed.

Statistical Analyses

We tested for the interactive effects of GKR presence (in vs. out of exclosures) and burrowing (on vs. off burrow mounds) on seedling establishment and soil properties using mixed-effects general linear models. Mixed-effects models allow for testing of crossed experimental treatments (i.e., fixed effects) while accounting for nonrandom associations among data from plots within sampling blocks (i.e., block random effects) (Bolker et al., 2009). Plant species, soil disturbance (mound vs. intermound), GKR presence, and all interaction terms were entered as fixed effects; site was entered as a block random effect; and establishment frequency was the response variable in the seedling establishment model. For soil properties, soil disturbance (mound vs. intermound) and GKR presence (as well as the interaction) were included as fixed effects and experimental site was included as a block random effect (Pinheiro and Bates, 2013). Each of 13 soil properties (see Table 2) was used as the response variable in separate models. We then used a Bonferroni-adjusted alpha level of 0.0038 to account for multiple tests. All analyses were conducted using the "nlme" package in program R (Pinheiro et al., 2013).

Results

Seed Predation and Seedling Establishment

Seed removal reduced seedling establishment of all four plant species by an average of 6.7% (Fig. 4A; range = 4–12% reduction, $F_{1,270} = 2.9$, $P = 0.09$). Although the effect of seed removal on establishment appeared to be stronger on burrow mounds than in the intermound areas (Fig. 5), the interaction between GKR presence and soil disturbance was not statistically significant ($F_{1,270} = 0.88$, $P = 0.35$). The impact of seed removal also did not vary significantly among plant species (species · GKR presence interaction $F_{3,270} = 0.13$, $P = 0.94$). However, the magnitude of the reductions in seedling establishment as a result of seed removal followed the same rank order as the selection ratios from the

Table 1

Diet selection by giant kangaroo rats *(Dipodomys ingens)* for seeds of 12 common plant species in the Carrizo Plain National Monument, California. Ratios were calculated on the basis of cafeteria-style diet trials ($n = 30$) conducted in 2008. Selection ratios > 1 indicate preference and ratios < 1 indicate avoidance. Species used in native seeding trials in this study are shown in bold

Species	Growth form	GKR selection ratio (95% CI)	Seed weight (mg)	Seed length (mm)
Lepidium nitidum	**Annual forb (native)**	**1.40 (1.26-1.54)**	**0.80**	**2.75**
Bromus madritensis spp. *rubens*	Annual grass (exotic)	1.24 (1.12-1.37)	1.59	8.27
Calandrinia ciliata	**Annual forb (native)**	**1.15 (0.99-1.32)**	**0.37**	**0.52**
Lasthenia californica	Annual forb (native)	1.14 (1.00-1.29)	0.76	3.19
Erodium cicutarium	Annual forb (exotic)	1.13 (1.02-1.24)	1.40	3.04
Schismus arabicus	Annual grass (exotic)	1.11 (0.95-1.26)	0.08	0.27
Festuca microstachys	**Annual grass (native)**	**1.05 (0.93-1.17)**	**0.81**	**3.97**
Hordeum murinum	Annual grass (exotic)	0.96 (0.84-1.09)	2.72	4.91
Amsinckia tessellata	Annual forb (native)	0.87 (0.76-0.97)	2.47	2.97
Tropidocarpum gracile	Annual forb (native)	0.80 (0.63-0.96)	0.26	1.47
Caulanthus lasiophyllus	Annual forb (native)	0.73 (0.61-0.84)	0.07	0.29
Poa secunda	**Perennial bunchgrass (native)**	**0.42 (0.28-0.55)**	**0.24**	**2.89**

Table 2
Soil physical and chemical properties in relation to the presence of giant kangaroo rats (in vs. outside exclosures) and their burrow mounds (intermound vs. burrow mound) in 2011 in the Carrizo Plain National Monument, California. Values are means ($n = 20$ experimental blocks) with standard errors in parentheses, and F values (with P values in parenthesis) from mixed-effects general linear models. Numerator and denominator degrees-of-freedom in all mixed models were 1 and 57, respectively. A Bonferroni-adjusted alpha level of 0.0038 was used to account for multiple tests. Statistically significant ($P < 0.0038$) differences are shown in bold

Soil characteristic	Means (Standard Errors)				*F* statistics (*P* values)		
	GKR Present		GKR Absent		Mound vs. intermound	GKR present vs. absent	Interaction
	Intermound	Burrow mound	Intermound	Burrow mound			
Bulk density ($g \cdot cm^3$)	1.73(0.03)	1.69 (0.04)	1.7 (0.02)	1.69 (0.03)	0.8 (0.37)	0.16 (0.69)	0.22 (0.64)
Exchangeable calcium (meq·100 g)	10.37 (0.59)	12.73 (1.07)	10.69 (1.03)	11.7 (1.13)	**11.95 (<0.0001)**	1.56 (0.22)	1.28 (0.26)
Cation Exchange Capacity (meq·100 g)	13.83 (0.87)	15.46 (1.19)	14.09 (1.21)	14.77 (1.28)	5.44 (0.02)	0.2 (0.66)	0.92 (0.34)
Electrical conductivity (dS·m)	0.38 (0.02)	0.59 (0.03)	0.4 (0.03)	0.53 (0.05)	**51.85 (< .0001)**	0.89 (0.35)	2.91 (0.09)
Bicarbonate/HCO3 (me·L)	2.19 (0.13)	2.73 (0.14)	2.07 (0.16)	2.4 (0.1)	**17.7 (<0.0001)**	4.9 (0.03)	0.99 (0.32)
Phosphorous-Olsen (ppm)	311.9 (24.71)	374.2 (20.48)	293.05 (21.65)	347.7 (29.98)	**10.76 (<0.0001)**	2.19 (0.14)	0.2 (0.66)
Exchangeable Magnesium (meq·100 g)	2.58 (0.32)	1.73 (0.19)	2.55 (0.34)	2.07 (0.33)	**47.33 (< .0001)**	1.01 (0.32)	4.13 (0.05)
Nitrogen-Nitrate (ppm)	1.74 (0.35)	3.88 (0.47)	1.76 (0.23)	2.71 (0.34)	**32.23 (< .0001)**	1.72 (0.2)	3.25 (0.08)
Exchangeable Sodium (ppm)	18.75 (10.66)	9.05 (2.17)	23.95 (17.07)	23.65 (15.56)	0.84 (0.36)	1.8 (0.18)	1.03 (0.31)
Organic Matter—Loss on Ignition (%)	1.5 (0.11)	1.67 (0.09)	1.37 (0.1)	1.47 (0.1)	**13.33 (<0.0001)**	**19.02 (<0.0001)**	1.16 (0.29)
Exchangeable Potassium (ppm)	12.05 (1.16)	13.15 (1.44)	11.36 (1.11)	12.09 (1.8)	0.19 (0.66)	1.1 (0.3)	0.2 (0.65)
pH	7.05 (0.05)	7.38 (0.06)	7.06 (0.07)	7.29 (0.07)	**34.66 (< .0001)**	0.7 (0.41)	1.26 (0.27)
Texture (% sand)	52.8 (3.14)	54.8 (3.22)	54.45 (3.72)	54.4 (3.28)	0.79 (0.38)	0.32 (0.57)	0.87 (0.35)

diet trials, with the most preferred species from the diet trials showing the greatest reduction in establishment due to seed removal (Fig. 4B).

Biotic Soil Disturbance and Seedling Establishment

Soil disturbance reduced seedling establishment of all four plant species by an average of 19.5% (Fig. 4A; range = 1–43% reduction, $F_{1,270} = 27.7, P < 0.0001$). The response of species to soil disturbance differed (species · disturbance interaction $F_{3,270} = 6.19, P = 0.0004$); *Poa secunda* was most affected (42.9% reduction) and *Festuca microstachys* was least affected (1.3% reduction; Fig. 4A). The effect of soil disturbance was similar within and outside of GKR exclosures (GKR presence · soil disturbance interaction $F_{1,270} = 0.88, P = 0.35$).

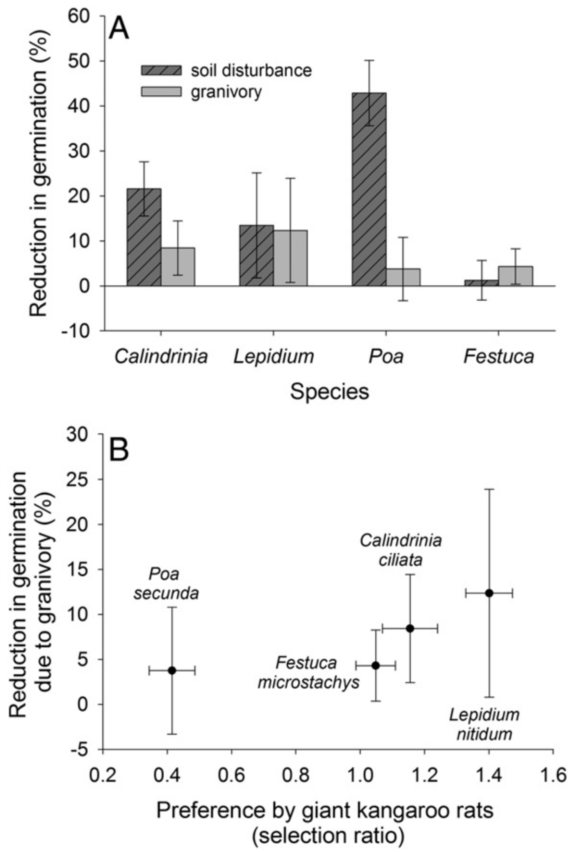

Fig. 4. Percent reductions in seed germination of four native species in rangeland restoration experiments in the Carrizo Plain National Monument, California. A, Reductions due to soil disturbance and seed removal by giant kangaroo rats. B, Effect of diet preference by giant kangaroo rats on the percent reduction in germination due to seed removal. Means and standard error bars are shown ($n = 38$ plots per comparison). Diet preferences were determined in cafeteria-style diet trials ($n = 30$).

GKR and Soil Properties

Burrow mound and intermound plots showed significant differences ($P < 0.0038$) in 8 of the 13 soil properties analyzed (Table 2). Nitrate levels were nearly twice as high on mound soils compared with intermound soils ($F_{1,59} = 30.68, P < 0.001$). Similarly, exchangeable calcium, electrical conductivity, bicarbonate, phosphorous, organic matter, and pH were all significantly higher on mound soils compared with intermound soils (Table 2). Only exchangeable magnesium was significantly lower on mound soils ($F_{1,59} = 44.94, P < 0.001$). Exchangeable sodium, exchangeable potassium, cation exchange capacity, bulk density, and texture showed no significant differences between soil disturbance treatments.

Organic matter was the only soil property significantly reduced by GKR exclusion, and no soil properties increased due to exclusion of GKR. There were no significant interactive effects of GKR exclusion and soil disturbance on soil properties (Table 2), indicating that four years of GKR exclusion (from 2007–2011) did not significantly reverse any of the observed differences in mound vs. intermound soil properties. However, differences in soil properties between mound and intermound soils were consistently lower where GKR had been excluded (see Table 2).

Discussion

Burrowing rodents are abundant throughout the southwestern United States and can have considerable effects on plant community composition and structure. Though rodent granivory has been widely acknowledged as a factor that could constrain native plant restoration success (Orrock et al., 2009; Orrock and Witter, 2010), granivory represents just one of many possible interactions between rodents and plant communities (Prugh and Brashares, 2012a). Other indirect interactions could be equally, if not more, important in altering restoration outcomes. Our work identifies one indirect effect, rodent-caused soil disturbance, as a significant factor controlling the assembly of native plants and affecting the outcome of restoration efforts. Although we found that seed removal reduced seedling establishment frequency, mixed-model results showed a stronger effect of soil disturbance compared with seed removal (6.7% vs. 19.5% reductions, respectively). Our

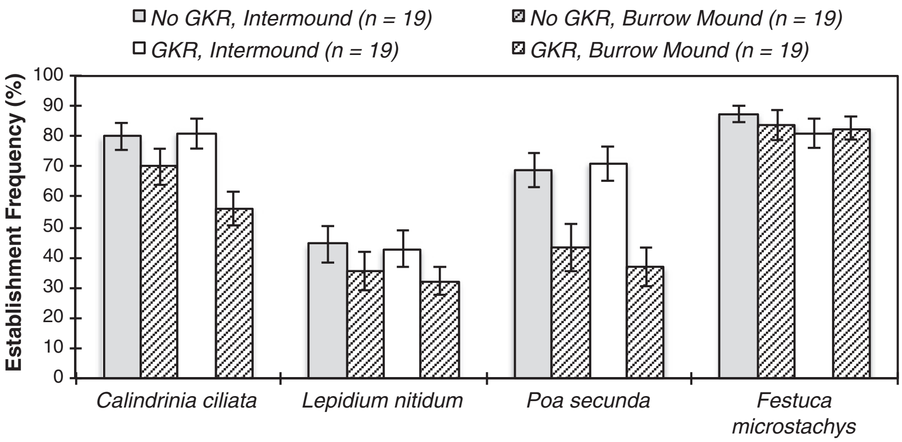

Fig. 5. Establishment frequency for seeds of four native plant species in response to seed removal and soil disturbance by giant kangaroo rats on restoration plots established in 2010 in the Carrizo Plain National Monument, California. Frequency counts were multiplied by 10 to obtain frequency percent. All bars are means ± standard error (SE).

study is among the first to explicitly consider the effects of biotic soil disturbance on restoration success and to compare the relative importance of an indirect effect, biotic soil disturbance, to the direct effect of seed removal. Although this study considered only one outcome variable, seedling establishment, the transition from germination to established seedling has been identified as the most important demographic bottleneck limiting the success of restoration seeding in grasslands (James et al., 2011).

Seed Removal

Our results are consistent with other studies of rodent effects on plant restoration, which have shown that granivory reduces seedling recruitment. However, the magnitude of seed removal effects documented in our study was far lower than that observed in other studies. In such studies, granivory by rodents was observed to have reduced seedling recruitment by approximately 30−70% (Hoffmann et al., 1995; Orrock et al., 2009). In our study, reductions in seedling establishment from seed removal ranged from 4–12% and were weakly associated with GKR seed preferences. The relatively weak association between seedling establishment success and GKR seed preferences may be due to the high density of GKR in the study area. The high density of GKRs could have resulted in competition for preferred seeds and greater use of nonpreferred seeds.

A likely reason for the discrepancy between our study and previous studies is the type of seeding method used. Our methods were consistent with restoration practices designed specifically to minimize seed predation and maximize seedling establishment. In systems with a high abundance of granivores, restoration practitioners often seed shortly after the first germinating rain in the late fall or early winter. Waiting until after the first germinating rainfall minimizes seed predation during the fall months when rodents are more active and allows managers to eradicate the first flush of weeds before seeding (Stromberg et al., 2007). Drill-seeding is also preferred over broadcast seeding as another means of reducing seed predation. Studies have shown that seeds on the soil surface are more susceptible to seed predation than those buried below the surface (Vander Wall, 1993. In this study, we used both relatively late (early winter) seeding and simulated drill seeding to approximate realistic restoration practices. In contrast, studies that found significant effects of granivory used broadcast seeding rather than drill seeding (Orrock et al., 2009) or sowed seeds earlier in the year when granivores may have been more active (Hoffmann et al., 1995).

Soil Disturbance

As expected, soil nutrient levels (particularly nitrate and potassium) were higher on burrow mounds compared with intermound areas. In addition, properties such as electrical conductivity, organic matter, and pH were also significantly different on burrow mound soils (Table 2). These findings are consistent with many other studies (e.g., Whitford and Kay, 1999) and suggest that both vertical transport and nutrient concentration are important factors affecting soil properties on GKR burrows. However, unlike other studies, we found no significant effect of rodent disturbance on soil bulk density. It is possible that differences in soil bulk density are isolated to the uppermost 2 cm to 3 cm of soil and that our soil cores (15 cm) were too deep to detect differences near the soil surface.

We expected that the exclusion of GKR could have affected soil properties via reductions in nitrogen (lack of fecal pellets), increased litter accumulation, and lack of sustained burrowing activity. However, differences in soil properties on plots in and out of GKR exclosures were minimal, and there were no interactive effects between GKR presence and soil disturbance treatments. These results indicate that burrowing has legacy effects on soil properties that can last for years after burrowing activities cease (Hastings et al., 2007). Legacy effects of burrowing rodent activity should therefore be considered in restoration treatments, in addition to other commonly considered legacies such as cultivation history (Stromberg and Griffin, 1996).

The importance of soil nutrient levels in altering the competitive balance between native and exotic plant species in grasslands has long been recognized (Weiss, 1999). The prevailing theory is that nutrient limitation creates an ecological filter that excludes the more generalist invasive species but allows more specialized native species to thrive under conditions of reduced competition (Corbin and D'Antonio, 2004; Nuttle, 2007). In response to this pattern, recent studies have investigated the potential role of soil amendments for increasing native plant restoration success (e.g., Bonebrake et al., 2011; Doll et al., 2011; Kulmatiski, 2011). Most commonly, soil nitrogen availability is reduced by adding carbon to the soil in the form of wood chips or glucose (Stromberg et al., 2007). Our results indicate that in some cases rodent disturbance may counteract these soil amendments and site preparation techniques by increasing nutrient availability.

Previous work has shown that exotic plants tend to outcompete native plants on GKR burrow mounds (Schiffman, 1994). Schiffman (1994) hypothesized that the differing species composition on burrow mounds was the result of selective granivory by GKR. However, our work indicates that differing soil properties may also play a large role. Even in the absence of competition (i.e., on our weeded plots), native seedling establishment was consistently lower on burrow mound plots compared with intermound plots. This result suggests that changes in the physical properties of soil may, in some cases, outweigh any direct benefits from increased soil nutrient levels. Specifically, soils on rodent-disturbed burrow mounds may desiccate more quickly and have lower soil moisture availability as a result of rodent disturbance, particularly in response to reduced bulk density and increased exposure to air. Several studies have documented lower soil moisture on burrow mound soils of kangaroo rats and other burrowing rodents compared with intermound areas (Sharma and Joshi, 1975; Mun and Whitford, 1990), and these findings are consistent with our field observation of highly exposed, desiccated soils on our burrow restoration plots (C.M. Gurney, personal observation).

The effect of soil disturbance by kangaroo rats on native seedling establishment varied considerably among species, with *Poa secunda* most negatively impacted and *Festuca microstachys* unaffected. Species used most often in rangeland restoration, such as native perennial bunchgrasses, may not be the most likely to succeed in areas with abundant burrowing rodents. Future research identifying native species with desirable ecosystem functions that also perform well on rodent-disturbed soils would help to improve restoration outcomes in these areas. In addition, restoration experiments conducted in rangelands with other species of burrowing rodents would help to assess the generality of our findings.

Implications

Burrowing rodents are ubiquitous in rangelands, and their effects on soil properties, especially nitrates, should be considered when calculating necessary soil amendments for native plant restoration. Soil disturbance by burrowing rodents can have stronger effects than seed removal on the establishment of native seedlings. Use of best practices such as late-season seeding and drill seeding may effectively reduce the impacts of granivory on seedling establishment, but burrowing rodents can leave lasting legacy effects on soil properties that inhibit seedling establishment of some native species. In areas with burrowing rodents, seeding with disturbance-tolerant native species may substantially increase restoration success.

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