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Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways

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Summary

1. Ecosystem engineers impact communities by altering habitat conditions, but they can also have strong effects through consumptive, competitive and other non-engineering pathways.

2. Engineering effects can lead to fundamentally different community dynamics than non-engineering effects, but the relative strengths of these interactions are seldom quantified.

3. We combined structural equation modelling and exclosure experiments to partition the effects of a keystone engineer, the giant kangaroo rat (*Dipodomys ingens*), on plants, invertebrates and vertebrates in a semi-arid California grassland.

4. We separated the effects of burrow creation from kangaroo rat density and found that kangaroo rats increased the diversity and abundance of other species via both engineering and non-engineering pathways.

5. Engineering was the primary factor structuring plant and small mammal communities, whereas non-engineering effects structured invertebrate communities and increased lizard abundance.

6. These results highlight the importance of the non-engineering effects of ecosystem engineers and shed new light on the multiple pathways by which strong-interactors shape communities.

Key-words: community structure, competition, *Dipodomys*, ecosystem engineer, facilitation, food web, habitat modification, indirect effects, keystone species, trophic effects

Introduction

Ecosystem engineers are defined as organisms that 'modulate resource availability (other than themselves) to other species by causing physical state changes in biotic or abiotic materials' (Jones, Lawton & Shachak 1994). While nearly all organisms can be viewed as ecosystem engineers to some extent (Wright & Jones 2006), engineers are considered keystone species if their impact is large relative to their abundance (Power *et al*. 1996). Ecologists have long recognized the ability of keystone engineers such as beavers (*Castor* sp.), burrowing rodents and large herbivores to dramatically affect community structure via their manipulation of the environment (Wright, Jones & Flecker 2002; Sinclair 2003; Davidson & Lightfoot 2006). However, keystone engineers also affect communities via interactions such as predation and competition, and we know remarkably little about how these non-engineering interactions compare in strength to the effects of habitat engineering.

While engineering and non-engineering pathways are often lumped together in studies of ecosystem engineers, they are likely to affect community structure in profoundly different ways. The habitat modification activities of most ecosystem engineers can result in long-lasting changes (e.g. creation of ponds, nesting cavities or tunnel networks) that are more stable over time than non-engineering interactions such as predation or competition, which will fluctuate with population sizes of engineers and their prey or competitors (Hastings *et al*. 2007). Furthermore, engineering can induce feedbacks that differ from non-engineering interactions in their timing, strength and direction (Jones *et al*. 2010). For example, the engineering activities of burrowing rodents such as prairie dogs (*Cynomys* spp.) have significant long-term benefits for species that rely on burrows but seldom construct them (e.g. many reptiles, burrow-nesting birds, small rodents; Lomolino & Smith 2004; Davidson, Lightfoot & McIntyre 2008b; Van Nimwegen, Kretzer & Cully 2008). However, these same beneficiaries may be negatively impacted on shorter time scales by the non-engineering activities of burrowing rodents that include burrow defence, removal of vegetation, predator attraction and the spread of parasites (Tabor *et al*. 1993;

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Heske, Brown & Mistry 1994; Davidson & Lightfoot 2006). Partitioning the net effects of keystone engineers into engineering and non-engineering components is, therefore, essential to predict how they alter community structure and dynamics over time.

Here, we quantify and partition the engineering and non-engineering effects of the giant kangaroo rat (*Dipodomys ingens*) on co-occurring species in a semi-arid grassland ecosystem. Kangaroo rats (*Dipodomys* spp.) are frequently characterized as keystone ecosystem engineers for their role in altering soil characteristics, changing habitat structure through grazing and creating expansive burrow networks that are used by many other species (Hawkins & Nicoletto 1992; Fields, Coffin & Gosz 1999). Kangaroo rats also have been shown to strongly affect plant and rodent communities through non-engineering pathways, most notably via competition and seed predation (Heske, Brown & Guo 1993; Valone & Brown 1995; Brock & Kelt 2004). We used surveys and experimental exclosures maintained over several years to isolate and quantify the relative strength of these engineering and non-engineering effects on the composition and dynamics of communities in which kangaroo rats occur. Specifically, we examined the engineering and non-engineering effects of the giant kangaroo rat on the abundance and diversity of lizards, squirrels, plants, invertebrates and birds at multiple scales, while controlling for primary productivity and variation in soils.

We hypothesized that engineering effects of giant kangaroo rats (i.e. burrow creation) would facilitate animal species known to benefit from subterranean habitat creation or soil disturbance, whereas non-engineering effects (i.e. interactions mediated by the presence or density of giant kangaroo rats) would suppress other granivores and herbivores through both interference and exploitative competition (Hawkins & Nicoletto 1992; Heske, Brown & Mistry 1994; Fig. 1). For plants, we predicted that giant kangaroo rat engineering would increase the abundance of exotic species and thereby reduce plant diversity, because soil disturbance favours dominance by invasive plants in our study system and others (Hobbs & Huenneke 1992; Schiffman 1994; Kotanen 1997). In contrast, we expected the non-engineering effects of giant kangaroo rats to increase plant diversity via reduction in dominant plant biomass and seeds (i.e. keystone predation; Paine 1969). For both plants and animals, therefore, we predicted opposing effects of giant kangaroo rat engineering and non-engineering interactions.

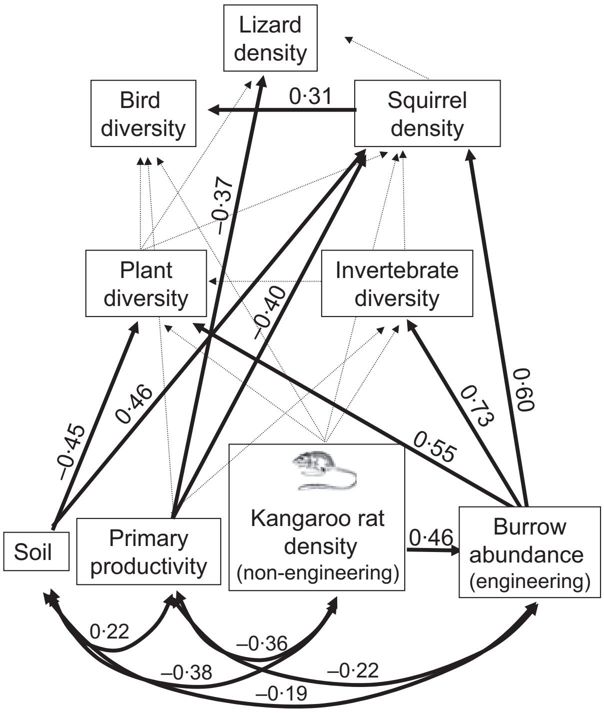

Fig. 1. Structural equation model estimating the relative importance of giant kangaroo rat engineering and non-engineering effects on grassland community structure in the Carrizo Plain National Monument, CA. Survey data from 30 2-ha sites spread across 112-km^2 were used to construct covariance matrices for the model. The model estimated the effects of kangaroo rat density (non-engineering effects), burrow density (engineering effects), primary productivity and soil characteristics on plant, bird, and invertebrate diversity, and squirrel and lizard density. Standardized path coefficients are shown, and significant paths are shown with solid arrows, and insignificant paths are shown with dotted arrows. Correlations among predictors are shown with curved double-headed arrows. The variable 'grassland type' was included in the model but is not shown here for simplicity (see Table 3 and Table S3, Supporting information for coefficients). Results from the year 2008 are shown here (see Table S3, Supporting information for coefficients estimated in 2007 and 2009).

Materials and methods

STUDY SPECIES

As its name implies, the giant kangaroo rat is the largest of the 21 kangaroo rat species (Plate 1a). Endemic to the San Joaquin Valley of California, giant kangaroo rats noticeably transform entire landscapes by creating prominent burrow mounds that are 7–10 m in diameter with similar spacing between mounds (Plate 1b,c). Each burrow mound consists of an extensive network of tunnels that extend more than three feet underground (L. R. Prugh, pers. obs.). Although federally endangered because of habitat loss, giant kangaroo rats can be locally abundant in remaining habitat, with densities up to 69 individuals per hectare (Prugh & Brashares 2010). They are treated as a keystone species in the multi-species recovery plan for this ecosystem (U.S. Fish and Wildlife Service 1998), but their effects on other species in the system have not been previously quantified.

STUDY AREA

This study took place in the Carrizo Plain National Monument (CPNM) in central California. The CPNM is a semi-arid grassland that receives an average of 232 mm of precipitation per year, falling almost exclusively as winter rain (California Data Exchange Center 2011). Historically, the CPNM was dominated by perennial bunchgrasses and native annual forbs, but today, the vegetative cover is dominated by European annuals such as barley (*Hordeum murinum*), red brome (*Bromus madritensis rubens*) and red-stemmed filaree (*Erodium cicutarium*) (Germano, Rathbun & Saslaw 2001). The

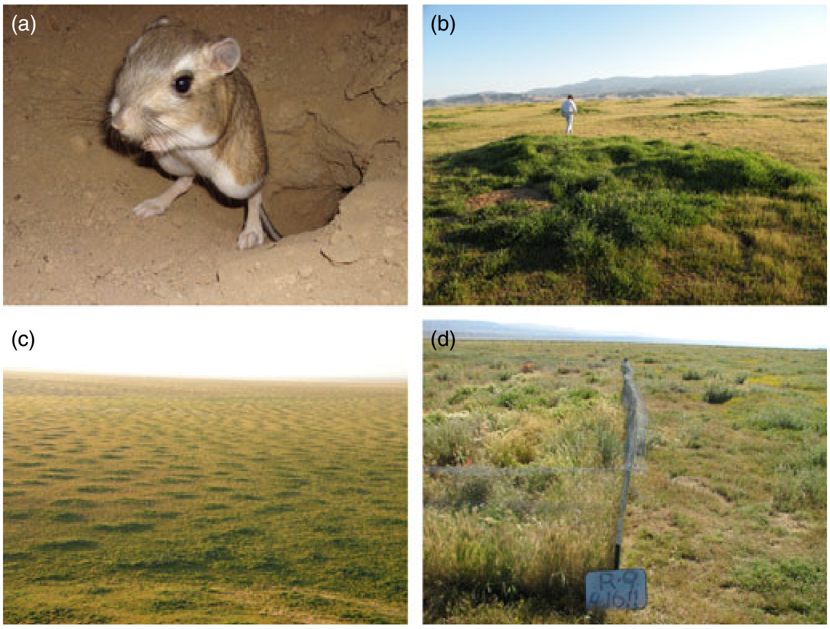

Plate 1. (a) A giant kangaroo rat, *Dipodomys ingens* (Photo credit: John Roser). (b) Close-up of a burrow mound (Photo credit: Donald Johnson). (c) Giant kangaroo rat burrow mounds in the Carrizo Plain National Monument, CA (Photo credit: Donald Johnson). (d) A kangaroo rat exclosure (Photo credit: John Chesnut).

CPNM harbours the largest remaining giant kangaroo rat population and is identified as a key conservation area for many state and federally listed species (U.S. Fish and Wildlife Service 1998). See Appendix S1 (Supporting information) for more information about the species in the Carrizo Plain grassland community.

STUDY DESIGN

Stratified randomization was used to place 30 2-ha (140 × 140-m) sites within two large pastures, covering a total area of 112 km^2 (Fig. S1, Supporting information). Both pastures were located within the core distribution of the giant kangaroo rat, lacked shrub cover, and were dominated by native and exotic annual forbs such as *Erodium circutarum* and *Lasthenia* spp. However, the pastures differed in grazing history and dominant grass type. The most common grass species in the pasture without recent grazing was a native, perennial bunchgrass (*Poa secunda*), whereas the pasture with recent grazing was dominated by several exotic annual grass species. Sites were established in both pastures (hereafter, 'perennial grassland' and 'annual grassland') to increase the generality of our findings. Ten sites were located in the perennial grassland, and 20 sites were located in the annual grassland. Ten of the annual grassland sites were established to examine cattle grazing effects, which were minimal during this study (L. R. Prugh & J. S. Brashares, unpublished analyses). Survey protocols were identical on all 30 sites. We partitioned the engineering and non-engineering effects of kangaroo rats on the grassland community in our study area using two general approaches: a large-scale observational approach and a small-scale experimental approach.

LARGE-SCALE OBSERVATIONAL APPROACH

We examined patterns of abundance and diversity in the grassland community across the 30 2-ha sites over a 3-year period (2007–2009). Giant kangaroo rat density was used as a proxy for non-engineering effects (range = 0–69 individuals per ha), and burrow density was used as a proxy for engineering effects (range = 11–243 burrows per ha). Thus, we assumed that the prevalence of non-engineering interactions (e.g. competition, seed predation) on a given site was a direct function of kangaroo rat density, and the prevalence of engineering effects was a direct function of burrow density. Burrow density was not strongly correlated with kangaroo rat density across sites in most years (r = 0·37, 0·69, 0·16 in 2007, 2008, and 2009, respectively).

We conducted annual surveys on each site to estimate the following parameters: the density of giant kangaroo rats, burrows, ground squirrels and lizards; biomass of vegetation and invertebrates; and diversity of plants, invertebrates and birds. Soil samples were also collected on each site in 2007. Preliminary examination of our survey data showed that ground squirrel density, lizard density, invertebrate species richness and plant diversity were positively correlated with giant kangaroo rat density across our study sites (Fig. S2, Supporting information). However, these community metrics were also correlated with soil properties and primary productivity (Fig. S2, Supporting information). We used structural equation modelling (SEM) to tease apart these correlations and estimate the relative importance of non-engineering effects (giant kangaroo rat density) and engineering effects (burrow density) on grassland community composition, while controlling for other site-specific factors (soil properties and primary productivity).

Structural equation modelling is a multivariate modelling approach that uses covariance matrices to evaluate hypotheses about dependence relationships among factors (Grace 2006). SEM is particularly useful when evaluating community dynamics, because each factor in an SEM may simultaneously function as a predictor and a dependent variable. An SEM consists of multiple linear regression equations that describe hypothesized relationships among factors, and these equations are solved simultaneously using maximum likelihood methods. The global fit of the model is evaluated using goodness-of-fit tests, and the strengths of interactions among factors are derived from the estimated regression coefficients. Covariance matrices were calculated based on survey data from each of the 30 2-ha study sites, and we specified interaction pathways in the SEM based on a-priori knowledge of this ecosystem and species life history traits (Appendix S1, Supporting information). Data from each year were analysed separately using a multi-group analysis; substantial variation in path strengths among years prevented the pooling of data among years. Analyses were conducted using AMOS software (Arbuckle 2009).

Giant kangaroo rat density, burrow density, soil properties [principal components analysis (PCA) axis 1] and primary productivity (peak vegetation biomass) were included in the SEM as correlated factors that affected plant diversity, invertebrate diversity, bird diversity, squirrel density and lizard density (Fig. 1). The correlations among predictors were specified in the model to account for likely feedbacks among these factors and allow estimation of their independent effects on community structure. The Shannon index (H') was used to calculate plant, invertebrate and bird diversity (Krebs 1999):

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i) \qquad \text{eqn 1}$$

where S is the number of species, and p_i is the proportion of the total sample made up of the ith species. SEM path coefficients and standard errors were estimated using maximum likelihood. The significance of direct, indirect and total effects of predictors on response variables was determined using Monte Carlo bootstrapping of unstandardized estimates with 1000 simulations. See Appendix S2 (Supporting information) for more details about the SEM.

SMALL-SCALE EXPERIMENTAL APPROACH

We used a kangaroo rat removal experiment as a second approach to examine giant kangaroo rat engineering and non-engineering effects on plants and invertebrates. We used a randomized block split-plot design with two factorial treatments: kangaroo rat presence (non-engineering effects) was the whole-plot factor and burrow presence (engineering effects) was the subplot factor, with two treatment levels (presence or absence) for each factor. There were 10 blocks in each grassland type, and replicate plant and invertebrate samples were obtained for each of the four treatment combinations in each block (Fig. S3, Supporting information).

A 20 × 20-m kangaroo rat exclosure was constructed in each of the 10 sites in the annual grassland and 10 sites in the perennial grassland ($n = 20$ exclosures, Plate 1d). Paired control plots (also 20 × 20-m) were located in a random compass direction 20 m from each kangaroo rat exclosure. Burrows made up approximately half the area of each exclosure and control plot. Although the exact locations of burrows could not be controlled experimentally, giant kangaroo rats are highly territorial (Cooper & Randall 2007), and the remarkably regular distribution and spacing of burrows (Plate 1c) indicate that burrow location was determined primarily by territoriality rather than microsite differences. Thus, we assumed that differences found in plant and invertebrate communities on and off burrows resulted from engineering activities, and differences found with and without kangaroo rats resulted from non-engineering activities. No pre-treatment differences in plant or invertebrate community variables within and outside of exclosures were detected (data from 2008 = pre-treatment, 2009 = post-treatment; Table S1, Supporting information), except that invertebrate diversity and orthopteran abundance were higher within exclosures pre-treatment (these trends reversed post-treatment, see Results).

Exclosure fencing was made of hardware cloth (mesh size = 0·2 cm) that extended 61 cm underground and 91 cm above ground, with a 15 cm overhang to prevent kangaroo rats from climbing into exclosures (Plate 1d). The exclosures presented a barrier to all kangaroo rats, but other vertebrates such as squirrels and lizards were observed easily climbing over and through the fencing. Exclosures were monitored for kangaroo rat activity on a monthly basis, and any kangaroo rats that had entered were removed prior to their re-establishment. Although other small mammals were also excluded, giant kangaroo rats completely dominated our study sites, and the effects of other species were likely minimal (Appendix S1, Supporting information).

Linear mixed model ANOVAS were used to analyse plant and invertebrate data collected within and outside of kangaroo rat exclosures. The exclosures were not effective until 2008 (Appendix S2, Supporting information), so data from 2009 only were used in analyses. Grassland type, giant kangaroo rat presence, burrow presence and their interactions were included as fixed effects, site was included as a random effect, and replicate within each treatment combination (four plant quadrats or two invertebrate pitfall traps; Fig. S3, Supporting information) was included as a nested random effect (Pinheiro & Bates 2000). Plant community response variables consisted of alpha diversity, richness, productivity, minimum biomass, native plant cover and exotic plant cover. Invertebrate community response variables consisted of alpha diversity, richness, biomass, beetle abundance, ant abundance and orthopteran abundance. Response variables were log-transformed to achieve normality when necessary. An adjusted alpha level of 0·008 was used to test for statistical significance to account for multiple tests (Bonferroni correction; Zar 1999). Analyses were conducted using program R (R Development Core Team 2010).

PLANT AND SOIL SURVEYS

Plants were surveyed on 400-m^2 plots within and outside of each exclosure on each site, and on the 10 annual grassland sites without exclosures ($n = 50$ survey plots total). Burrows were mapped in each survey plot, and four 1-m^2 quadrats were randomly located on burrows, and four quadrats were located off burrows ($n = 8$ quadrats per survey plot; 400 quadrats total). To avoid fence effects, quadrats were not placed within one metre of the exclosure fencing. Plant composition was determined in April each year using the pinframe sampling method (Seabloom *et al.* 2003), wherein the plant species intersecting each of 81 cross-hairs were identified. For the SEM, in which the unit of replication was the 2-ha site ($n = 30$), plant composition data collected on and off burrows on each site were pooled, and data collected within exclosures were not included. Because plant composition differed substantially on and off burrows, the pooled site-level plant diversity estimates in the SEM were analogous to gamma (regional) diversity.

Primary productivity was estimated by clipping vegetation in a 1/16-m^2 quadrat adjacent to each 1-m^2 quadrat when biomass was at its peak in April (prior substantial grazing by kangaroo rats or other species). We also estimated plant biomass at its minimum in October each year, after kangaroo rats had clipped vegetation and prior to germination of the next year's plant crop. Clip plot locations were rotated each session so that the same spot was never clipped more than once. Biomass samples were dried for 48 h at 65 °C and weighed.

One burrow quadrat and one non-burrow quadrat in each survey plot were randomly chosen for soil analysis ($n = 100$ soil samples). A 4·6-cm diameter, 20-cm deep soil core was taken adjacent to each quadrat, and samples were analysed by the ANR Laboratory at UC Davis for chemical composition (N, C, Bray-P, Ca, Mg, HCO_3, Na, Cl), texture (per cent clay, silt and sand), salinity (SP and EC) and pH. PCA was used to reduce the number of soil variables while maximizing the information retained. The first PCA axis retained 58·7% of variation across the 14 variables and was highly correlated with per cent sand ($r = 0·89$). This axis was used in statistical analyses to represent soil properties.

INVERTEBRATE SURVEYS

Pitfall traps were used to collect invertebrates in June ($n = 8$ traps per site, 240 traps total). Four traps were inside and four were outside each exclosure, with half of the traps on burrows and half off burrows. Traps were separated by at least five metres. Plastic cups (0·47-L size) were buried such that the top of the cup was level with the ground, and propylene glycol was added to a depth of 2 cm. After 2 weeks, traps were removed and invertebrates were rinsed and stored in 50-mL falcon tubes filled with ethanol. All invertebrates were counted and identified to order and morphotype. Morphotypes roughly corresponded to unique species; invertebrate diversity was, therefore, calculated at the species level for each pitfall sample. Because species were identified to morphotype, invertebrate diversity could be calculated for individual samples only and could not be pooled to estimate gamma diversity. In the SEM, therefore, diversity estimates from replicate invertebrate samples were averaged on each 2-ha site (excluding samples collected within exclosures), and invertebrate diversity in the SEM was, therefore, an estimate of average alpha (local) diversity rather than gamma diversity. Samples were weighed after an half an hour of surface drying to estimate invertebrate biomass.

VERTEBRATE SURVEYS

We conducted annual kangaroo rat, ground squirrel, bird and reptile surveys on each site. Giant kangaroo rat density was estimated in August using 3–5 day mark-recapture surveys. Sherman traps (38·1 cm long) were placed every 20 m on a 100 × 100-m grid, with each trapline offset such that traps were arranged in a draughtboard ($n = 60$ traps per site, diagonal trap distance = 14·1 m). Traps were baited with sterilized parakeet seed (primarily millet), set at dusk and checked between 23:00 and 04:00 h. Processing of captured individuals consisted of weighing, PIT- and ear-tagging, measuring skull length and determining sex and reproductive status. Their burrows were mapped and coded as active or inactive based on the presence or absence of fresh digging and tracks.

San Joaquin antelope squirrel (*Ammospermophilus nelsoni*) density was estimated in May using 5-day mark-recapture surveys. Tomahawk traps were placed every 40 m on a 100 × 100-m grid, with traps arranged in a draughtboard ($n = 18$ traps per site, diagonal trap distance = 28·3 m). Traps were covered with burlap to provide shade, set at dawn, and checked every 2 h until noon or the temperature rose above 32 °C. Population estimates of kangaroo rats and squirrels were calculated in program R (R Development Core Team 2010) using the ‘RDHet’ model (robust design with heterogeneity) in the RMark package (Laake & Rexstad 2008). These estimates were very precise (mean CV = 4%, range = 0·03–26%, $n = 180$ estimates) because of high recapture rates.

Lizard density was estimated using replicated visual line transect surveys in June ($n = 3$ surveys per site, 90 total). Seven 140-m-long transects spaced 20 m apart were slowly walked by a single observer, and all reptiles detected within 10 m on either side of each transect were identified and recorded, along with the perpendicular distance from the transect line. Nearly, all reptiles recorded were side-blotched lizards (*Uta stansburiana*; Appendix S1, Supporting information). Density estimates were obtained using the program DISTANCE (Thomas *et al*. 2006).

Bird diversity was estimated using replicated point count surveys during the breeding season in April ($n = 4$ surveys per site, 120 total). Counts were conducted between 06:00 and 09:00 h and lasted 10 min. All birds seen and heard during this time were identified and recorded.

Predators could not be surveyed adequately on our 2-ha sites because they ranged too widely and occurred at relatively low densities. We counted San Joaquin kit foxes (*Vulpes macrotis mutica*) seen on our sites as well as the number of kit fox faeces deposited on our traps and neither index correlated with any other variables or improved models. Therefore, predators were not included in the present study.

Results

LARGE-SCALE OBSERVATIONAL APPROACH

The structural equation model explained a substantial amount of variation in community structure across our large (2-ha) study sites for most years (Table 1). Because of high variability among years, the global goodness-of-fit test for the multi-year SEM indicated significant deviations between the model and the data, but tests of single-year models with significant paths only did not show significant lack of fit (Table S2, Supporting information).

The net effect of giant kangaroo rats on gamma plant diversity, alpha invertebrate diversity, lizard abundance and squirrel abundance was positive, whereas kangaroo rat effects on bird diversity were negligible (Fig. 1, Table 2). These positive effects were mainly because of engineering: the SEM indicated that engineering effects (burrow creation) resulted in higher gamma plant diversity, alpha invertebrate diversity and squirrel density, with average total standardized effects of 0·35–0·61 (Table 3). Giant kangaroo rat engineering had a stronger effect on these variables than non-engineering effects mediated by giant kangaroo rat density or other site characteristics (soil properties, primary productivity and grassland type; Table 3, Fig. 1). Paths between either engineering or non-engineering effects and all measures of community structure (except bird diversity) were positive and significant in most years, with coefficients ranging from 0·26 to 0·73 (Table S3, Supporting information).

Non-engineering effects on lizards were positive and stronger than engineering effects (coefficients = 0·32 and 0·04, respectively; Table 3). In contrast, the path from squirrels to lizards was negative in 2007 and 2008 (−0·46 and −0·30, respectively), indicating that squirrels may suppress lizard numbers through either competition or predation. The path from giant kangaroo rat density to

Table 1. The amount of variance (R^2) in response variables explained by the structural equation model each year

	Year		
Response variable	2007	2008	2009
Invertebrate diversity	0·78	0·37	0·67
Plant diversity	0·58	0·67	0·57
Squirrel density	0·32	0·48	0·19
Lizard density	0·86	0·64	0·71
Bird diversity	0·70	0·44	0·29

Table 2. Summary of the engineering, non-engineering and net effects of giant kangaroo rats on components of the grassland community, synthesizing results from the large-scale observational approach and the small-scale experimental approach

Taxon	Response metric	Engineering effect	Non-engineering effect	Net effect
Invertebrate	Biomass	None	+	+
	Alpha diversity/richness	+	+	+
Plant	Productivity	+	None	+
	Alpha diversity/richness	–	None	–
	Gamma diversity	+	+	+
Lizard	Density	+	+	+
Squirrel	Density	+	–	+
Bird	Diversity	–	+	None

A '+' indicates a positive effect, '–' indicates negative effect, and 'none' indicates no effect. For plants, the large-scale approach examined gamma diversity, and the small-scale approach examined alpha diversity. For invertebrates, both approaches examined alpha diversity.

Table 3. Total, direct and indirect effects of predictor variables on response variables in the structural equation model (see Fig. 1)

		Predictor variable							
Response variable	Effect type	Grassland type	Kangaroo rat density	Burrow density	Soil	Primary productivity	Invertebrate diversity	Plant diversity	Squirrel density
Invertebrate diversity	Total	0·36	0·25	0·37	0·27	−0·26	–	–	–
Plant diversity		−0·10	0·43	0·61	−0·28	−0·03	0·17	–	–
Squirrel density		0·03	0·13	0·35	0·14	−0·23	0·31	−0·07	–
Lizard density		0·52	0·32	0·04	−0·38	−0·03	−0·07	0·02	−0·32
Bird diversity		−0·49	0·03	−0·09	0·06	0·18	−0·11	−0·08	−0·10
Invertebrate diversity	Direct	−0·11	0·09	0·37	0·27	−0·26	–	–	–
Plant diversity		−0·18	0·17	0·53	−0·33	–	0·17	–	–
Squirrel density		−0·27	−0·06	0·29	0·02	−0·12	0·33	−0·07	–
Lizard density		0·64	0·20	0·20	−0·33	−0·05	0·03	0·01	−0·32
Bird diversity		−0·55	0·09	−0·03	–	0·21	−0·05	−0·06	−0·10
Invertebrate diversity	Indirect	0·47	0·16	–	–	–	–	–	–
Plant diversity		0·08	0·26	0·08	0·05	−0·03	–	–	–
Squirrel density		0·30	0·19	0·06	0·12	−0·11	−0·02	–	–
Lizard density		−0·12	0·11	−0·16	−0·05	0·02	−0·10	0·01	–
Bird diversity		0·06	−0·06	−0·06	0·06	−0·04	−0·07	−0·02	–

Standardized effects are shown, which represent the change in the response variable given a standard deviation change in the predictor. Total effects are the sum of direct and indirect effects. A dash (–) indicates the path was not included in the model. Average effects are shown for years 2007–2009 (see Table S3, Supporting information for annual effects). A positive effect for grassland type indicates higher diversity or density in annual grasslands, whereas a negative effect indicates an association with perennial grasslands. Positive soil effects roughly indicate higher diversity or density in sandy soils, and negative effects indicate an association with soils that have higher clay content.

squirrels was negative but not significant in 2007 and 2008 (−0·17 and −0·05, respectively), indicating competitive effects were weak (Table S3, Supporting information). Grassland type was the main factor affecting bird diversity (Table 3).

SMALL-SCALE EXPERIMENTAL APPROACH

Plant communities differed on and off burrows (i.e. with and without engineering by kangaroo rats), while invertebrate communities differed within and outside of kangaroo rat exclosures (i.e. with and without non-engineering effects). No significant interactions were detected among the engineering and non-engineering treatments, indicating that engineering effects were similarly strong in the presence and absence of kangaroo rats, and non-engineering effects were similarly strong on and off burrows. See Table S4 (Supporting information) for a summary of statistical results.

Alpha plant diversity was not strongly affected by giant kangaroo rat engineering or non-engineering interactions (Fig. 2a). Plant richness was lower in areas with engineering (on burrows) and also tended to be lower in areas with non-engineering effects (i.e. where giant kangaroo rats were present; Fig. 2b). Non-engineering interactions did not affect primary productivity (Fig. 2c), but minimum plant biomass was lower where non-engineering effects were present (Fig. 2d). Primary productivity was higher in areas with engineering (Fig. 2c), and minimum biomass tended to be higher with engineering even though giant kangaroo rats had clipped and removed much of the vegetation (Fig. 2d).

Native and exotic plants were impacted differently by engineering and non-engineering interactions. As predicted, exotic cover was higher in areas with engineering (Fig. 2f). The overall effect of engineering on native cover was not significant (Fig. 2e), but native cover was negatively affected by engineering in the perennial grassland (Table S4a, Supporting information). Non-engineering interactions reduced native cover but did not affect exotic plant cover (Fig. 2e,f).

Non-engineering interactions strongly affected invertebrate community structure, whereas engineering had little effect (Fig. 3). Alpha invertebrate diversity was not affected by either engineering or non-engineering interactions (Fig. 3a). Non-engineering interactions increased invertebrate richness (Fig. 3b), invertebrate biomass (Fig. 3c) and beetle abundance (Fig. 3d). Both engineering and non-engineering effects tended to increase orthopteran abundance (Fig. 3e). Neither engineering nor non-engineering interactions affected ant abundance (Fig. 3f).

Discussion

This study found that both non-engineering and engineering effects of an ecosystem engineer were important in determining community composition. Our results are aligned with a burst of recent research documenting strong effects of ecosystem engineers on marine, freshwater and terrestrial communities (e.g. Wright 2009; Breitburg *et al.* 2010; Ward & Ricciardi 2010). We partitioned the keystone effects of giant kangaroo rats into engineering and non-engineering components and used both a multi-year observational approach and an experimental approach to examine community structure. Both lines of evidence showed strong effects of kangaroo rats via engineering and non-engineering pathways, and the relative importance of each pathway differed among taxonomic groups in the grassland community.

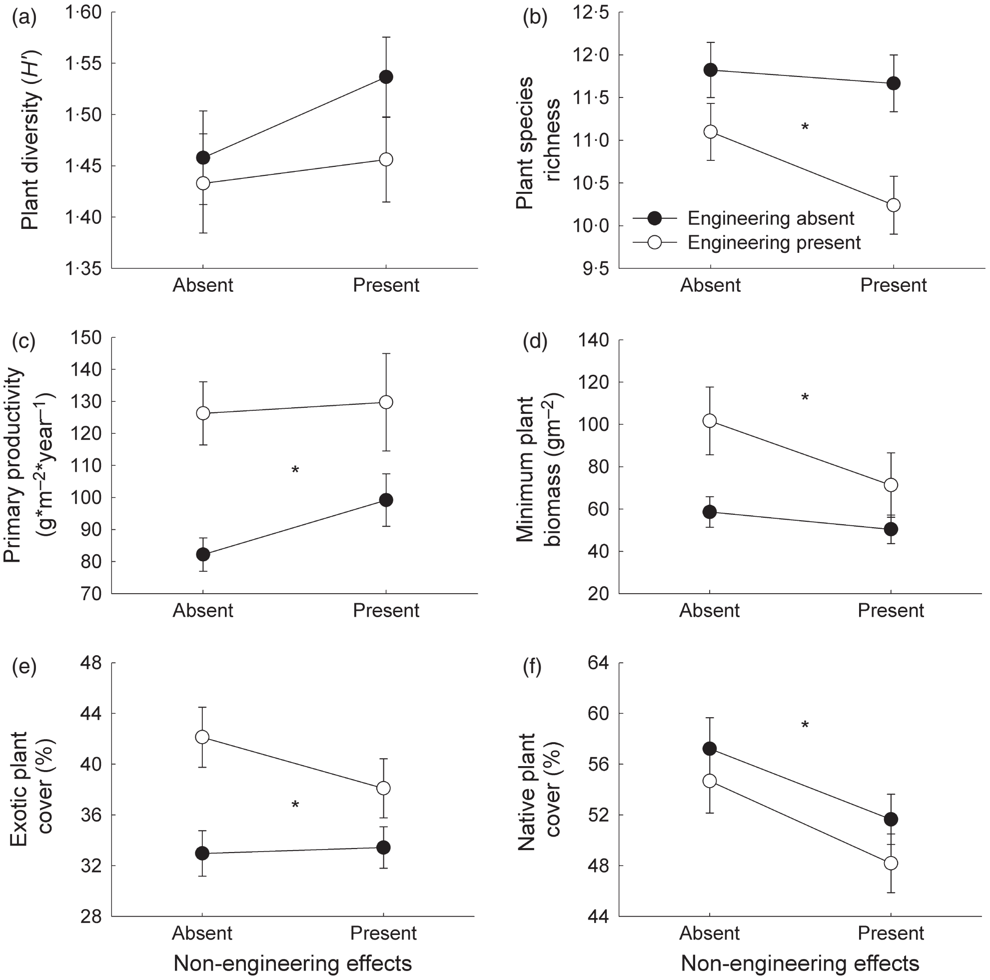

Fig. 2. Effect of giant kangaroo rat engineering and non-engineering interactions on plant (a) diversity, (b) richness, (c) primary productivity, (d) minimum plant biomass, (e) exotic cover and (f) native cover in the Carrizo Plain National Monument, CA. Species diversity (alpha) was calculated using the Shannon index (*H′*). Means and standard errors are shown from quadrats in areas with engineering present (on burrows, open circles) and absent (off burrows, closed circles) in 20 kangaroo rat exclosures ('non-engineering absent') and 20 paired plots where kangaroo rats occur ('non-engineering present'). Significant engineering effects are shown with an '*' between the lines, and significant non-engineering effects are shown with an '*' above the lines. Significance was evaluated at $\alpha = 0{\cdot}008$ (Bonferroni corrected).

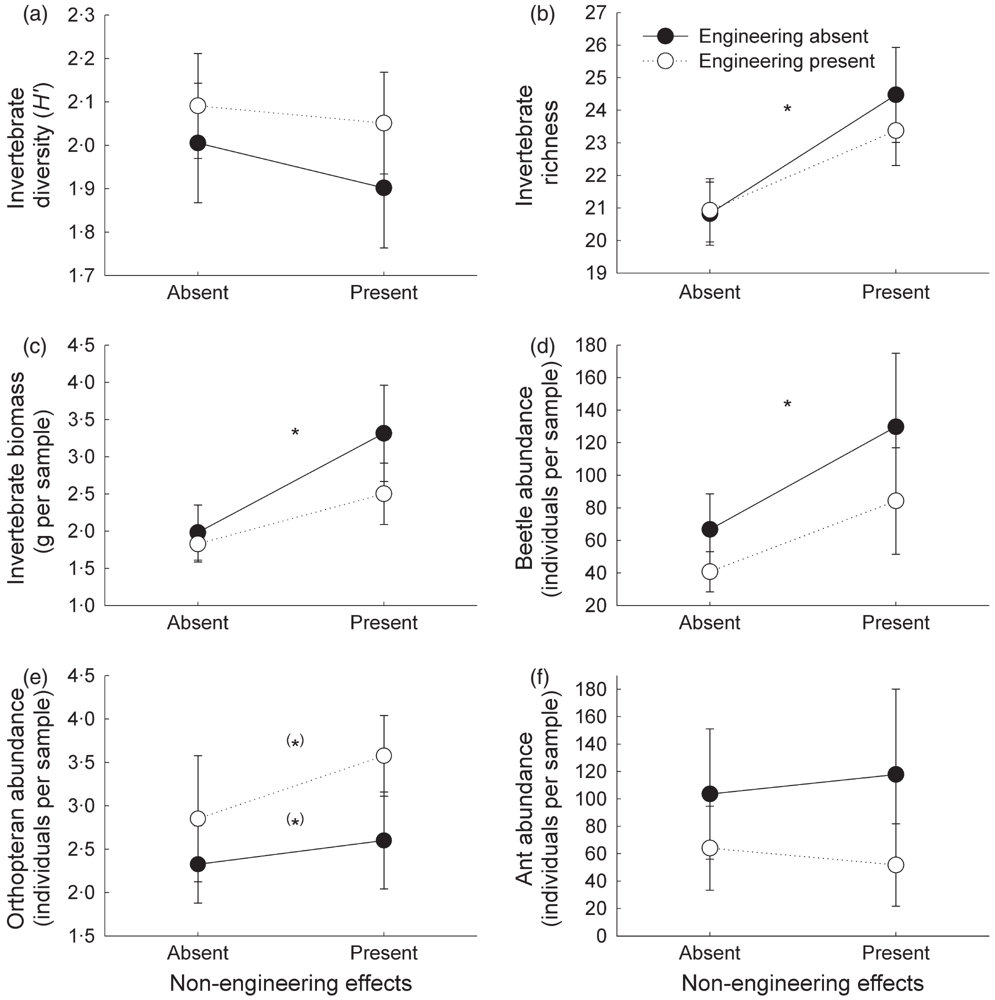

Fig. 3. Effect of giant kangaroo rat engineering and non-engineering interactions on invertebrate (a) diversity, (b) richness and (c) biomass, and on the abundance of (d) beetles, (e) orthopterans (grasshoppers, crickets, and katydids) and (f) ants in the Carrizo Plain National Monument, CA. Species diversity (alpha) was calculated using the Shannon index (*H′*). Means and standard errors are shown from pitfall trap samples in areas with engineering present (on burrows, open circles) and absent (off burrows, closed circles) in 20 kangaroo rat exclosures ('non-engineering absent') and 20 paired plots where kangaroo rats occur ('non-engineering present'). Significant engineering effects are shown with an '*' between the lines, and significant non-engineering effects are shown with an '*' above the lines. Significance was evaluated at $\alpha = 0{\cdot}008$ (Bonferroni corrected). (*) Significance at the $\alpha = 0{\cdot}05$ level.

While engineering by giant kangaroo rats in the CPNM was the primary factor structuring the plant community and determining squirrel abundance, non-engineering interactions strongly influenced invertebrate community structure and lizard abundance. Overall, facilitation via both engineering and non-engineering pathways had stronger effects on most species than soil properties, primary productivity or negative interactions such as competition. These findings, therefore, failed to support our prediction that engineering and non-engineering effects would oppose one another (Sanders & van Veen 2011). Instead, our results support theoretical predictions that engineering promotes coexistence among competitors (Gross 2008) and raise the possibility that coexistence can be promoted by a single species via multiple pathways. Because engineering effects can outlast the engineers themselves (Hastings *et al.* 2007) and are, therefore, relatively stable over time, species primarily affected by kangaroo rat engineering should be less influenced by fluctuations in kangaroo rat density compared to species primarily affected by non-engineering interactions (e.g. competition, predation, food subsidization).

VERTEBRATE COMMUNITY STRUCTURE

The response of vertebrates demonstrated the complex interactions that were mediated simultaneously by giant kangaroo rat engineering and non-engineering pathways. For the state-threatened San Joaquin antelope squirrel, the creation of burrow mounds by giant kangaroo rats had a stronger effect on their abundance than grassland type, soil properties or primary productivity, and the positive effect of this ecosystem engineering outweighed the weak competitive effect of giant kangaroo rats. Like squirrels, lizards were often seen using burrows as refuges from predators and heat, and we, therefore, expected lizards to respond positively to engineering as well (Davidson, Lightfoot & McIntyre 2008b). However, squirrels appeared to negatively affect lizards, resulting in an indirect negative effect of giant kangaroo rat engineering that largely cancelled out its direct positive effect (Table 3). When squirrel numbers were relatively low in 2007, lizards did indeed appear to benefit from engineering (Table S3, Supporting information). Surprisingly, we found that non-engineering effects facilitated increased lizard density, perhaps because their food abundance (invertebrates) was markedly higher in the presence of giant kangaroo rats.

Not all vertebrates responded strongly to giant kangaroo rats, however. Engineering appeared to negatively affect bird diversity in 2007 but had no effect in 2008 and 2009, and non-engineering interactions had no effect on birds in any year. We obtained similar results when examining bird abundance rather than diversity. As with previous studies (MacArthur & MacArthur 1961; Willson 1974), we found instead that bird diversity was higher in areas with more variable habitat structure (perennial grasslands) and higher productivity.

Many predators in the Carrizo Plain rely on giant kangaroo rats as a food source (J. Castillo, unpublished manuscript), and predators such as kit foxes, burrowing owls, badgers, snakes and weasels modify and take over giant kangaroo rat burrows. Because these predators occur at relatively low densities and range over wide areas, we were not able to quantify their response to giant kangaroo rats in the current study. Likewise, giant kangaroo rats were the only nocturnal rodents captured on our sites (except for four short-nosed kangaroo rats, *D. nitratoides*), thus precluding examination of giant kangaroo rat effects on other nocturnal rodents. This domination may be due to the requirement of shrub cover by smaller rodents (Rosenzweig & Winakur 1969), because shrubs were absent on our sites. However, strong competitive effects of large kangaroo rats on smaller rodents were found during a long-term experiment in the Chihuahuan desert (Heske, Brown & Mistry 1994), so it is also possible that giant kangaroo rats have competitively excluded other species. Thus, while we found that facilitation by giant kangaroo rats swamps the effects of competition with other granivores in the extant community, competition could play an important role in maintaining exceptionally low rodent diversity in the open grasslands of the Carrizo Plain.

PLANT COMMUNITY STRUCTURE

Our large-scale and small-scale approaches both detected stronger effects of engineering than non-engineering interactions on plant community structure. Likewise, Wilby, Shachak & Boeken (2001) found that engineering effects of porcupines (*Hystrix indica*) and harvester ants (*Messor* spp.) on plants were stronger than trophic effects. Our small-scale approach showed that plant productivity was markedly higher in areas with engineering (on burrows), likely because of modified soil conditions (L. R. Prugh, unpublished data; Canals, Herman & Firestone 2003). Contrary to expectations, our large-scale approach showed that sites with extensive giant kangaroo rat engineering (i.e. high burrow density) had relatively high gamma plant diversity, and this effect was strong during all 3 years (Table S3, Supporting information). We expected burrow creation to result in lower plant diversity because soil disturbance should have led to domination by exotics (Hobbs *et al.* 1992). Indeed, our small-scale approach showed that engineering decreased plant richness (although alpha plant diversity was not affected) and increased exotic plant cover. This pattern supports findings from a previous study comparing plant cover on- and off-giant kangaroo rat burrows (Schiffman 1994). Engineering, therefore, appears to create stable heterogeneity in the landscape that increases beta plant diversity, which may explain the positive effect of engineering on gamma diversity despite its negative effect on alpha diversity (Davidson & Lightfoot 2008a). Additionally, the edge habitat created by burrows may create micro-ecotones that increase gamma diversity (Harrison 1997).

The structural equation model showed that non-engineering effects of giant kangaroo rats increased gamma plant diversity in 2008 and 2009, supporting our hypothesis that seed predation and herbivory by giant kangaroo rats would increase plant diversity by suppressing dominant species. However, our exclosure experiments showed that non-engineering effects decreased the cover of native rather than exotic plants. This finding contrasts with results from a study in the Chihuahuan desert, where large kangaroo rats reduced the cover of large-seeded exotic plants (Guo *et al.* 1995). Overall, native plant cover was actually higher than exotic cover in our study area (53% vs. 37% cover, respectively), which is unusually high for an arid California grassland where native cover rarely exceeds 20% (Bartolome *et al.* 2007). Non-engineering interactions such as seed predation may, therefore, have led to increased diversity by suppressing dominant native plants rather than exotics.

INVERTEBRATE COMMUNITY STRUCTURE

In contrast to responses of the plant community, our exclosure experiments showed that non-engineering effects of giant kangaroo rats had a strong impact on invertebrate community structure, whereas engineering effects were relatively small. After merely 1 year of excluding kangaroo rats, beetle abundance was nearly half the level where kangaroo rats were present. Invertebrate biomass and richness also sharply declined, and orthopterans were less abundant without giant kangaroo rats. Because orthopterans are herbivorous, and 90% of the beetles and ants in our study were granivorous or herbivorous (Appendix S1, Supporting information), we had expected giant kangaroo rats to suppress the abundance of these species via competition. Instead, giant kangaroo rats facilitated increased abundance of orthopterans and beetles and had no effect on ants. By clipping vegetation and storing large quantities of seeds in surface caches and below ground (Shaw 1934), kangaroo rats may provide a substantial food subsidy to these species. Caching and hoarding species such as kangaroo rats and squirrels may, therefore, function as 'keystone subsidizers'. Although much attention has been given to cross-ecosystem resource subsidies (Polis, Anderson & Holt 1997; Marczak, Thompson & Richardson 2007), within-system subsidies may play an important and underappreciated role in community dynamics.

While our small-scale approach indicated that giant kangaroo rat engineering had minimal effects on invertebrate diversity, our large-scale approach found that diversity was higher on sites with relatively extensive engineering in 2007 and 2008. Studies have likewise found that engineering by prairie dogs (*Cynomys* spp.) and bannertail kangaroo rats (*D. spectabilis*) increases invertebrate diversity (Bangert & Slobodchikoff 2006; Davidson & Lightfoot 2007). The discrepancy between our large and small scale results may be due to the high mobility of invertebrates relative to the small-scale mosaic of burrow and non-burrow areas (Plate 1b). Thus, positive effects of engineering may only be detectable over a relatively large scale.

LARGE- VS. SMALL-SCALE APPROACHES

Ecologists have long recognized the importance of scale in ecology (Wiens 1989; Sandel & Smith 2009). Using survey data from large and small plots distributed over a 112 km^2 area, we obtained greater insight into community dynamics than if we had used only one approach. The SEM allowed us to tease apart correlations among vertebrate species that ranged too widely to manipulate experimentally, but we could not infer strong causality because the input data were observational. Additionally, results from SEMs are trustworthy only when key factors are included and models are properly constructed (Smith, Brown & Valone 1997; Grace & Pugesek 1998; Grace 2006). We included soil characteristics and primary productivity to account for their influences on the community, but it is possible that factors we were unable to include, such as predator density, were also important drivers. The exclosure experiment allowed us to make stronger causal inferences about the effects of kangaroo rats on plants and invertebrates because we directly manipulated kangaroo rat presence. Examining plant and invertebrate diversity at both scales revealed contrasting patterns of engineering effects on alpha and gamma plant diversity and also highlighted the scale dependency of engineering effects on invertebrates.

INTERANNUAL VARIABILITY

We detected strong effects of giant kangaroo rats on the grassland community, but these effects often varied annually (Table S3, Supporting information). Arid grasslands are characterized by non-equilibrium dynamics that are strongly influenced by climatic factors, particularly precipitation conditions (Vetter 2005). Precipitation did not vary spatially among our study sites, but the timing and amount of rainfall varied annually. Although we cannot test for climatic effects with only 3 years of data, we suspect that stochastic variation in rainfall may explain at least some of the variability in community dynamics among years. Interestingly, variable interaction strengths can actually increase community stability over time (Kokkoris *et al.* 2002; Navarrete & Berlow 2006). Additional years of data are needed to adequately examine the effect of climatic variability on interaction strengths and stability in our grassland system.

FACILITATION CASCADES

Recently, several studies have reported the triggering of facilitation cascades by ecosystem engineers, whereby a basal habitat former facilitates an intermediate ecosystem engineer, which leads to increased abundance or diversity of other species at higher trophic levels (Altieri, Silliman & Bertness 2007; Thomsen *et al.* 2010). We found little support for the existence of facilitation cascades among the species included in our study. That is, the engineering and non-engineering effects of giant kangaroo rats on community structure attenuated quickly and were largely unmediated by other factors. For example, engineering increased plant diversity each year, but increased plant diversity did not appear to affect bird diversity, lizard density or squirrel density in any year (Fig. 1). Identifying the conditions under which facilitation cascades are expected to result from ecological perturbations, and predicting the altered dynamics that may result, would greatly advance our understanding of community dynamics.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Map of study area.

Fig. S2. Bivariate correlations among community variables.

Fig. S3. Diagram of a study site.

Table S1. Tests for pre-treatment differences in plant and invertebrate communities.

Table S2. Goodness of fit tests for the structural equation model.

Table S3. Direct, indirect, and total effects, 2007–2009.

Table S4. Summary of ANOVA results.

Appendix S1. Selected species life history traits.

Appendix S2. Supporting methods.