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Environmental gradients determine the potential for ecosystem engineering effects

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Understanding processes that determine biodiversity is a fundamental challenge in ecology. At the landscape scale, physical alteration of ecosystems by organisms, called ecosystem engineering, enhances biodiversity worldwide by increasing heterogeneity in resource conditions and enhancing species coexistence across engineered and non-engineered habitats. Engineering–diversity relationships can vary along environmental gradients due to changes in the amount of physical structuring created by ecosystem engineering, but it is unclear how this variation is influenced by the responsiveness of non-structural abiotic properties to engineering. Here we show that environmental gradients determine the capacity for engineering to alter resource availability and species diversity, independent of the magnitude of structural change produced by engineering. We created an experimental rainfall gradient in an arid grassland where rodents restructure soils by constructing large, long-lasting burrows. We found that greater rainfall increased water availability and productivity in both burrow and inter-burrow habitats, causing a decline in local (alpha) plant diversity within both of these habitats. However, increased rainfall also resulted in greater differences in soil resources between burrow and inter-burrow habitats, which increased species turnover (beta diversity) across habitats and stabilized landscape-level (gamma) diversity. These responses occurred regardless of rodent presence and without changes in the extent of physical alteration of soils by rodents. Our results suggest that environmental gradients can influence the effects of ecosystem engineering in maintaining biodiversity via resource heterogeneity and species turnover. In an era of rapid environmental change, accounting for this interaction may be critical to conservation and management.

Keywords: arid grassland, biodiversity, burrowing rodents, community composition, disturbance, endangered species, rainfall gradient, resource availability, soil properties

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Introduction

Ecosystem engineering interactions between species are ubiquitous in ecological systems (Jones et al. 1994). These interactions occur when organisms alter the physical environment and indirectly affect responding species (Jones et al. 2010). While species often respond directly to engineering-induced changes in structural abiotic properties, ecosystem engineering effects are also mediated by non-structural abiotic properties that are impacted by the altered physical environment, such as changes in chemistry or the distribution of water (Jones et al. 2010). Around the globe, ecosystem engineering interactions are important for maintaining habitat heterogeneity and biodiversity across landscapes (Jones et al. 1997, Hastings et al. 2007, Cavieres and Badano 2009). Biodiversity is enhanced because ecosystem engineering creates habitats with different resource conditions than surrounding habitats, resulting in landscapes in which a greater number of species can co-occur (Levin 1974, He and Bertness 2014, McIntire and Fajardo 2014). Much study has been devoted to examining variability in biodiversity responses to ecosystem engineering (Wright and Jones 2004, McIntire and Fajardo 2014, Romero et al. 2015), particularly along environmental gradients (Wright et al. 2006, Cavieres and Badano 2009, He and Bertness 2014). As engineering species' densities and traits vary along environmental gradients, the amount of physical change created by these species varies as well, resulting in altered effects on the abiotic environment and responding species (Schob et al. 2013, Bulleri et al. 2016). For instance, cushion plants increase in size and branch density with increasing elevation, and concomitantly, these nurse plants have greater effects on soil properties and stronger facilitation of other plants (Schob et al. 2013). While differences in the magnitude of structural change clearly impact the strength of engineering effects on biodiversity, it is unclear how variation in the responsiveness of non-structural abiotic properties affects engineering–biodiversity relationships along environmental gradients.

In this study, we asked whether the strength of ecosystem engineering–biodiversity relationships varies along an environmental gradient, even in the absence of changes in the amount of physical alteration due to ecosystem engineering. We hypothesized that engineering effects on resource conditions and biodiversity become stronger as the potential for non-structural abiotic change becomes greater, analogous to the potential energy of a physical system (Rankine 1853). As potential energy is the stored energy that an object possesses due to its relative position in a system, the capacity for ecosystem engineering to change a local environment is due to its position on environmental gradients. For example, engineering that restructures soils and indirectly decreases soil water content may have little effect on soil moisture under drought conditions when a decrease in soil moisture is restricted, and a larger effect on soil moisture as drought is alleviated. As environmental heterogeneity increases with greater differences in abiotic properties between engineered and non-engineered habitats, we may expect landscape-level biodiversity to increase as well. Similar to potential energy, we propose that differences in the potential for non-structural abiotic change can be measured by comparing the change in abiotic conditions due to engineering (a constant structural change) at different points along an environmental gradient. If these differences have a large impact on ecosystem engineering outcomes, then efforts to accurately predict biodiversity responses to engineering along environmental gradients must account for both the amount of physical alteration produced by ecosystem engineering and the capacity for non-structural abiotic change to occur in response to engineering.

To test our hypothesis, we manipulated rainfall in an arid annual grassland in California, where giant kangaroo rats *Dipodomys ingens* excavate large burrows that may last for decades (Whitford and Kay 1999) and that affect soil resource availability for plants (Gurney et al. 2015). Burrowing increases water infiltration to deep soil layers, causing drier soil conditions in the rooting zone relative to inter-burrow soils (Whitford and Kay 1999). Moreover, burrow soils have higher inorganic nitrogen (N) content (Gurney et al. 2015), but plants need adequate soil moisture to access this N (He and Dijkstra 2014). As rainfall varies greatly in California grasslands, we expected this environmental gradient would alter the capacity for burrowing to change soil water and N availability for plants. Creating an artificial rainfall gradient in plots spanning kangaroo rat burrow and inter-burrow habitats, we anticipated that as rainfall increased, greater potential for non-structural abiotic change would cause larger differences between burrow and inter-burrow soils and plant diversity responses would intensify.

In addition, we expected the above dynamics irrespective of the presence of kangaroo rats and changes in their burrow maintenance and seed-foraging activities. We tested this by excluding kangaroo rats from half of the experimental plots (Prugh and Brashares 2012) at all rainfall levels. Furthermore, though giant kangaroo rat abundances increase following high rainfall (Bean et al. 2014) and increased abundances may intensify their effects on vegetation (Meserve et al. 2003, Madrigal et al. 2011), the rainfall manipulations occurred on too small a scale to influence the kangaroo rat population. Thus, the influence of precipitation on kangaroo rat density-mediated effects on plants were minimal in our experiment. Moreover, burrow position in the landscape is stable through time (Grinath et al. 2018) and the kangaroo rats primarily maintain pre-existing burrows over multiple generations (Cooper and Randall 2007), rather than excavating new burrows and changing the amount of burrow structure in the landscape.

To assess biodiversity responses to rainfall and ecosystem engineering, we evaluated how plant alpha diversity within engineered and non-engineered habitats (i.e. on/off burrows) scaled to landscape-level gamma diversity via species turnover, or beta diversity, between these habitats (Whittaker 1972, Anderson et al. 2011). Regardless of whether greater rainfall results in increased or decreased alpha diversity within

burrow and inter-burrow habitats, we expected that ecosystem engineering would enhance beta and gamma diversity (Jones et al. 1997, Hastings et al. 2007, Cavieres and Badano 2009) and that these effects would become stronger with greater rainfall. While previous studies have shown that ecosystem engineering effects on biodiversity depend on changes in non-structural abiotic properties across environmental gradients (Wright et al. 2006, Schob et al. 2013), to our knowledge, this study is the first to demonstrate that these dynamics occur independent of changes in engineered structures.

Material and methods

Experimental design

Our study was conducted at the Carrizo Plain National Monument, CA (35°35'N, 120°04'W, elevation = 700 m); home to the largest remaining population of the federally endangered giant kangaroo rat (Williams and Kilburn 1991). This arid grassland ecosystem primarily consists of annual plants, which grow during the cool, wet Mediterranean winter (growing season from October to April); little grows during the hot, dry summer. We used kangaroo rat burrowing as a natural experiment, contrasting burrow and inter-burrow habitats. We also manipulated rodent presence to understand how kangaroo rat burrow maintenance and seed foraging influenced the effects of burrows and rainfall on plant diversity. At each of 18 sites, we used 400-m² rodent exclosures (which primarily manipulated kangaroo rats) and paired control plots to evaluate the effects of kangaroo rat presence (Prugh and Brashares 2012). The exclosures were established in the summer of 2008 and were continuously maintained through data collection in spring 2016.

We manipulated rainfall across the kangaroo rat experimental conditions using 100-m² rainout shelters constructed of acrylic shingles, which have been shown to have negligible impacts on air and soil temperatures (Yahdjian and Sala 2002), and paired solar-powered sprinkler systems (using water collected from shelters). We redistributed 50% of rainwater at 12 experimental sites; remaining 6 sites received ambient precipitation (Supplementary material Appendix 1 Fig. A1). Half the shelters were located in rodent exclosures and redistributed rainfall to rodent control areas; the other half were in rodent control plots and shunted water to exclosures. Rainfall treatments were assigned to sites using a stratified random design, with random assignments within groups of three neighboring sites that had similar vegetation. The rain redistribution systems were installed in summer 2014 and manipulated rainwater from October through March in the two growing seasons prior to this study. From 1995 to 2016, cumulative rainfall from October to March was 18.8 cm on average (Supplementary material Appendix 1 Fig. A2a, MesoWest CAZC1, 35°10′N, 119°77′W). Total growing season rainfall preceding data collection in this study was 12.8 cm (Supplementary material Appendix 1 Fig. A2b). Therefore, the manipulations created conditions of approximately 6.4 and 19.2 cm rainfall, resulting in a rainfall gradient extending from drought to average conditions.

We measured soil properties and plant assemblages to evaluate abiotic resource and diversity responses to rodents and rainfall. Equaling the size of the rainfall treatments (100 m²), we established 36 plots across the rainfall and rodent manipulations (2 plots site^{-1}). Plots contained both burrow and inter-burrow habitats at approximately a 50/50 ratio (Gurney et al. 2015). In each plot, we randomly established eight 1-m² sampling quadrats stratified between burrow and inter-burrow habitats (n = 288 quadrats, Supplementary material Appendix 1 Fig. A1).

Within the quadrats, we measured soil resources important for plant growth, including soil water content and inorganic N availability. Soil water was measured as volumetric water content (VWC) from the top 15 cm of soil, the primary rooting zone, using a modified HydroSense II. We constructed a standard curve relating the VWC readings taken from the HydroSense with the factory-provided 12 cm soil probes, to 'period' measurements taken by replacing the probes with 15 cm long nails. The nails were inserted into the ground and contact was made with the sensor by replacing the manufactured probes with steel bolts in the sensor head and pressing the bolts against the nail heads. The sensor sends an electrical pulse through the soil probes and measures the amount of time (i.e. period) that it takes for the pulse to return to the sensor; the greater the soil water content, the longer it takes for an electrical pulse to travel the length of the probe because water draws away the electrical current. These period measurements recorded from the nails were then transformed into permittivity values (Ka) and then finally VWC values using the relationship: $VWC = 0.007576 \times Ka^2 + 0.5480 \times Ka - 0.3906$ ($p < 0.001$, $R^2 = 0.99$). This relationship was calibrated by taking measurements with both the factory-supplied probes and the nails in the same soil across a wide range of moisture values. In mid-March 2015, we placed a set of nails in each vegetation quadrat and recorded VWC on 19–20 March, just prior to removal of the rain redistribution system. We also recorded VWC after the rainfall manipulation was disabled, on 28 March, 12 April, 27 April and 10 May. In preliminary tests, slight variability in nail length and mass had little effect on soil moisture measurements taken from the nails, so we did not correct for this variation in the nails.

We measured soil inorganic N content in 6 of 8 quadrats per plot in mid-April, at the height of the growing season. Two 15 × 2.2 cm soil cores were collected from the outside edge of the quadrats, combined, sieved (2 mm) and then inorganic N was extracted using 2 M KCl (following Robertson et al. 1999). Because we were at a remote field location, we had to adjust our extraction methods and attempted to minimize the effects of these changes on our data. Firstly, all funnels and flasks were washed in 1.2 M HCl prior to conducting the extractions; weigh boats and sieves were cleaned with ethanol and a wire brush between samples. Because deionized

water was unavailable for N extraction, distilled water was substituted. To account for ions present in the distilled water, we ran control blanks with the deionized water, which we extracted. These values were subtracted from all soil extractions and did not interfere with our evaluation of relative differences in N availability across the experimental factors. Soil extractions were analyzed for nitrate-N using a flow injection module, and for ammonium-N with a multi-detection microplate reader at the University of Colorado Boulder.

In addition to measuring pools of inorganic N, we conducted in situ field incubations to measure N mineralization (Robertson et al. 1999). In every 100-m² plot, two soil cores (15 cm depth) on burrows and two off burrows were placed in polyethylene bags, and reburied. We began the field incubations after several days of rainfall when VWC levels were elevated, ensuring that soil moisture was adequate to support mineralization (Supplementary material Appendix 1 Fig. A2). After approximately 30 days, the buried bags were collected and inorganic N was extracted as above, combining cores within habitat in each plot for the extractions (n = 46). Some samples were damaged by rodents and were not included in extractions. To determine net N mineralization, total inorganic N (nitrate plus ammonium) in May was subtracted from that in April (averaged across quadrats within plots) and then divided by the total number of days in the field incubation.

To determine plant responses, we measured plant species cover and primary production for every 1-m² quadrat in April. We estimated cover of all plant species using an 81-point pinframe method (Prugh and Brashares 2012). In addition to the species recorded under each point in the pinframe, we noted the occurrence of additional species that were within quadrats but not under pin points. To include these species, we recorded species presence as a single pin hit within the quadrat, adding one observation to all species under pins. In effect, a species could have a maximum of 82 observations m^{-2}. Aboveground net primary production was estimated by sampling all aboveground biomass in a 0.25×0.25 m² area adjacent to the western edge of the 1-m² quadrat, drying at 65°C for 48 h, and weighing. Because all aboveground vegetation senesces in this annual grassland, aboveground biomass in April is approximately equivalent to annual production, assuming little herbivory. Most rodent herbivory occurred after we sampled biomass (Grinnell 1932).

Statistical analysis

We analyzed the data in R ver. 3.2.3 (<www.r-project.org>). At the quadrat level, we used linear mixed effects models (LMMs) to evaluate responses of soil properties, productivity, plant species densities and Shannon evenness (E). In the models, fixed effects consisted of rainfall (continuous), rodent burrowing (binary: off/on burrow), rodent presence (binary: excluded/present), and all interactions among these three factors. Nested random effects consisted of experimental site and plot, where quadrat-level observations occurred in plots nested within sites (Zuur et al. 2009). We performed LMMs with random intercepts for unbalanced data (type II SS) using the 'lme' and 'Anova' functions from the R packages 'nlme' and 'car', respectively. To account for unequal variances across treatment levels, we performed a model selection procedure to find the optimal variance structure for each model (Zuur et al. 2009). We fit models with seven different variance structures (none; identity structure for rodent presence, burrowing and their combination, and fixed, power or exponential structures for rainfall), and selected the best model based on lowest Akaike information criterion (AIC) values and evaluation of the residuals. Though we preferred not to transform data, some data were necessarily LN-transformed (plus 1) to meet assumptions of normality in the models. On rare occasion, we removed extreme outlying points from the data to achieve appropriate model fit; these points were well outside the range of other points based on visual analysis of boxplots and were likely the result of measurement error. Six of the 288 quadrats had soil water concentrations that were extremely high, potentially due to leaks in the rainfall treatment or water pooling next to soil probes. Thus, we restricted all analyses to the remaining 282 quadrats for which accurate soil moisture data were available (based on the VWC measurement prior to removing the rainwater manipulation).

We rarefied (Gotelli and Colwell 2001) plant cover data to obtain abundance-corrected measures of alpha and gamma diversity (Supplementary material Appendix 1 Fig. A3), using plot-level data and the 'rarefy' function from the 'vegan' package in R. Rarefaction was performed because more species are likely to be observed with greater cover, which covaries with plant abundances in our grassland system (pin hits recorded separate individuals). To obtain plot-level data for alpha diversity within habitats, in each plot we aggregated data across burrow quadrats and across inter-burrow quadrats separately. Gamma diversity was measured from data aggregated across all quadrats within plots. Multiplicative beta diversity was then calculated at the plot scale as gamma richness divided by the mean alpha richness (average of alpha diversity on and off burrows within each plot) across burrow and inter-burrow habitats (Whittaker 1972, Anderson et al. 2011). One experimental plot was excluded from the beta and gamma analyses because no data were available on burrow; another plot was withheld because there were too few data to obtain rarefied estimates (n = 34 plots). Rarefied diversity data were analyzed with the same LMM methods described above, with the exception that rodent burrowing was not included as a factor in analyses of beta and gamma diversity.

To further assess how beta diversity responded to rainfall and rodents, we conducted multivariate hypothesis tests, coupled with ordination to visualize the multivariate results (Anderson et al. 2006, 2011, Anderson and Walsh 2013). We measured differences in community composition with Bray–Curtis dissimilarities calculated from relative cover data. For each community observation, relative cover was measured as each species' pin count divided by the total pin count for all species, effectively removing the influence of the abundance

gradient resulting from the rainfall manipulation. Because multivariate community analyses can be skewed by extremely rare species, prior to measuring dissimilarities we removed species that were present in only one or two communities. To evaluate whether rainfall, burrowing, rodent presence, or their interactive effects altered the average composition of the plant assemblage, we used permutational multivariate ANOVA (PERMANOVA: function 'adonis') to assess differences in multivariate centroids among groups. Site was included as a block effect in the PERMANOVA using the 'strata' command. To test whether rainfall, burrowing and rodent presence influenced dispersion in community composition (beta diversity), we conducted separate permutational multivariate analyses of dispersion (PERMDISP: function 'betadisper') for each experimental factor. Continuous explanatory variables cannot be used for the analyses of dispersion; therefore, we specified precipitation as a nominal variable in the analyses. To visualize the PERMANOVA and PERMDISP results, we used a 2-axis non-metric multidimensional scaling (NMDS: function 'metaMDS') ordination. We used 99% SE ellipses to depict levels for the burrow factor within the NMDS and contours to show the influence of the rainfall gradient. To understand how community composition and the experimental factors covaried with the soil properties, we used the 'envfit' function to fit soil properties (using plot-level data) to the ordination, shown as arrow vectors within the NMDS. Additionally, we visualized differences in community dispersion across the experimental factors with boxplots. We used the 'vegan' package in R to conduct these tests with 999 permutations.

Lastly, we used indicator species analyses (Dufrene and Legendre 1997) to evaluate which species caused changes in community composition on and off burrows under the different rainfall conditions. Indicator species analyses assess the 'indicator value' for each species across experimental groups based on the species' fidelity and relative abundance (or cover). We conducted permutational indicator species analyses with the 'multipatt' function from the 'indicspecies' package (10 000 permutations), using the same data included in the multivariate analyses above. These tests were conducted for the six experimental levels corresponding with the burrowing×rainfall conditions, which was appropriate for identifying species that were significant indicators of burrow or inter-burrow habitats under high, ambient or low rainfall. Throughout all the analyses, results were considered significant if $p \leq 0.05$.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.gk1r3s5> (Grinath et al. 2019).

Results

Soil resource availability diverged between burrow and inter-burrow habitats as rainfall increased (Fig. 1, Supplementary material Appendix 1 Table A1). Soil water content increased

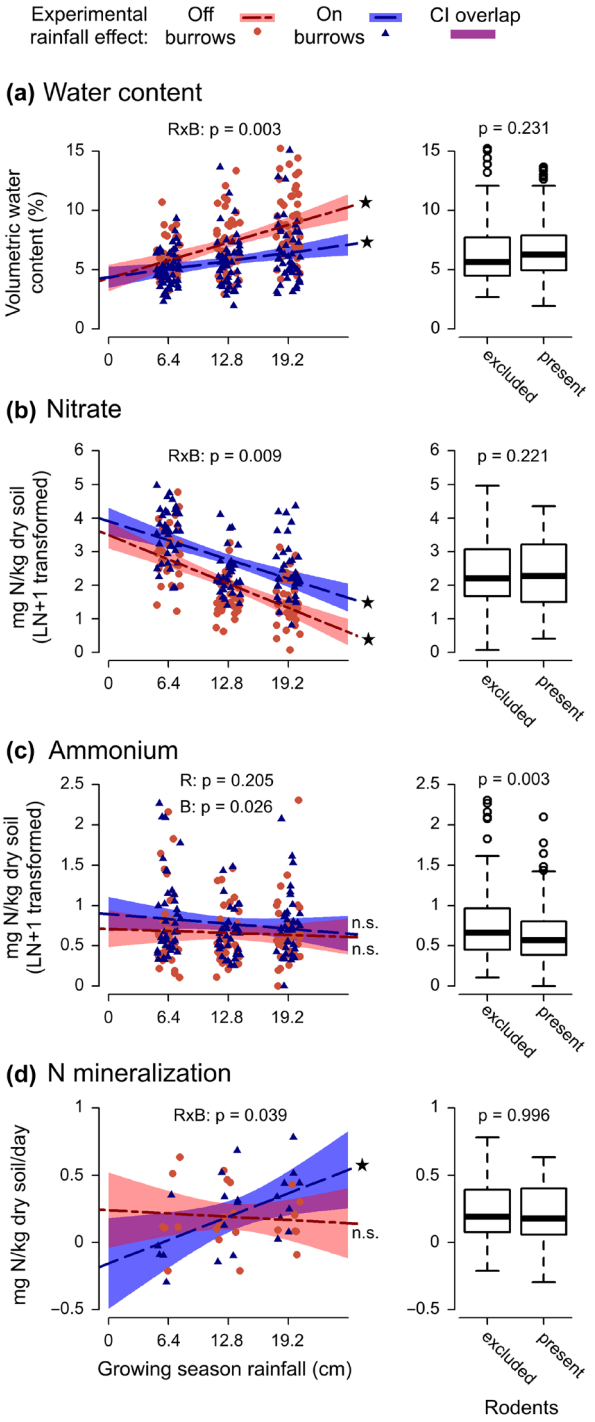

Figure 1. Soil (a) moisture, (b) nitrate, (c) ammonium and (d) nitrogen mineralization responses to rainfall manipulations, rodent burrowing and rodent presence. p-values shown (R: rainfall, B: burrowing, RxB: interaction) are from linear mixed effects models. Rainfall and burrowing effects are visualized with post hoc regressions with 95% confidence intervals; effects of rodent presence are shown with boxplots. Significant post hoc regressions (slope: $p \leq 0.05$) are indicated by stars. The y-intercepts are not significant in the post hoc regressions in (d). Points are jittered at each rainfall level to depict y-axis variability.

with greater rainfall in both habitats and was lower on burrows; however, the difference in soil water content between habitats became greater with increasing rainfall (Fig. 1a). Similarly, burrowing had a larger effect on soil nitrate levels with increasing rainfall, though overall, nitrate decreased with more rainfall (Fig. 1b). Burrow engineering also increased soil ammonium content, but this was not affected by rainfall (Fig. 1c). Lastly, there were greater differences in net N mineralization with greater rainfall (Fig. 1d). While N mineralization off burrows was negligible under all rainfall conditions, this N cycling rate became greater on burrows with more rainfall. There were no statistical interactions between rodent presence and burrowing or rainfall; thus, rodent presence did not alter the effects of burrow engineering and rainfall on soil properties (Supplementary material Appendix 1 Table A1). While the effects of rodent presence on soil properties were mostly non-significant, ammonium levels were lower when rodents were present compared to when they were excluded (Fig. 1c).

The landscape-level effect of burrow engineering on plant diversity also increased with additional rainfall, despite growing species dominance within habitats (Fig. 2, Supplementary material Appendix 1 Table A2). A list of plant species and their average relative cover off and on burrows is provided in Table 1. Rarefied alpha diversity within both burrow and inter-burrow habitats declined with greater rainfall (Fig. 2a). Additional analysis at the scale of 1 m^2 quadrats revealed that alpha diversity decreased as plants became more dominant within habitats (Supplementary material Appendix 1 Table A3). Although species densities per square meter increased with greater rainfall (LMM: $\chi^2 = 6.59$, $p = 0.010$), along with greater aboveground net primary production in both habitats (rainfall × burrowing interaction LMM: $\chi^2 = 4.67$, $p = 0.031$, Supplementary material Appendix 1 Fig. A4a), species evenness decreased with more rainfall (LMM: $\chi^2 = 29.06$, $p < 0.001$, Supplementary material Appendix 1 Fig. A4b). In contrast, beta diversity between habitats increased with greater rainfall (Fig. 2b). As a consequence of the opposing patterns in alpha and beta diversity, gamma diversity did not change across the rainfall gradient (Fig. 2c). The presence of rodents did not influence the effects of burrowing and rainfall on these diversity measures (Supplementary material Appendix 1 Table A2). However, alpha diversity tended to be greater in the presence of rodents (Fig. 2a), as was primary production and species evenness (Supplementary material Appendix 1 Fig. A4). There were no effects of rodent presence on beta or gamma diversity (Fig. 2b–c).

We further evaluated the result that beta diversity increased with greater rainfall by examining community dissimilarities across the experimental conditions, visualized by NMDS in Fig. 3a–e. Analyses of dissimilarities show that beta diversity increased with higher rainfall: greater dispersion in dissimilarities (i.e. beta diversity: Anderson et al. 2011) occurred under wet conditions (PERMDISP: $F = 4.92$, $p = 0.012$, Fig. 3f, Supplementary material Appendix 1 Table A5). The NMDS shows this dispersion as two separate clines increasing in opposite directions from near the center of the plot (upper-right versus lower-left in Fig. 3c). One of these clines aligns with the change in average composition caused by kangaroo rat burrowing (PERMANOVA: $F = 6.53$,

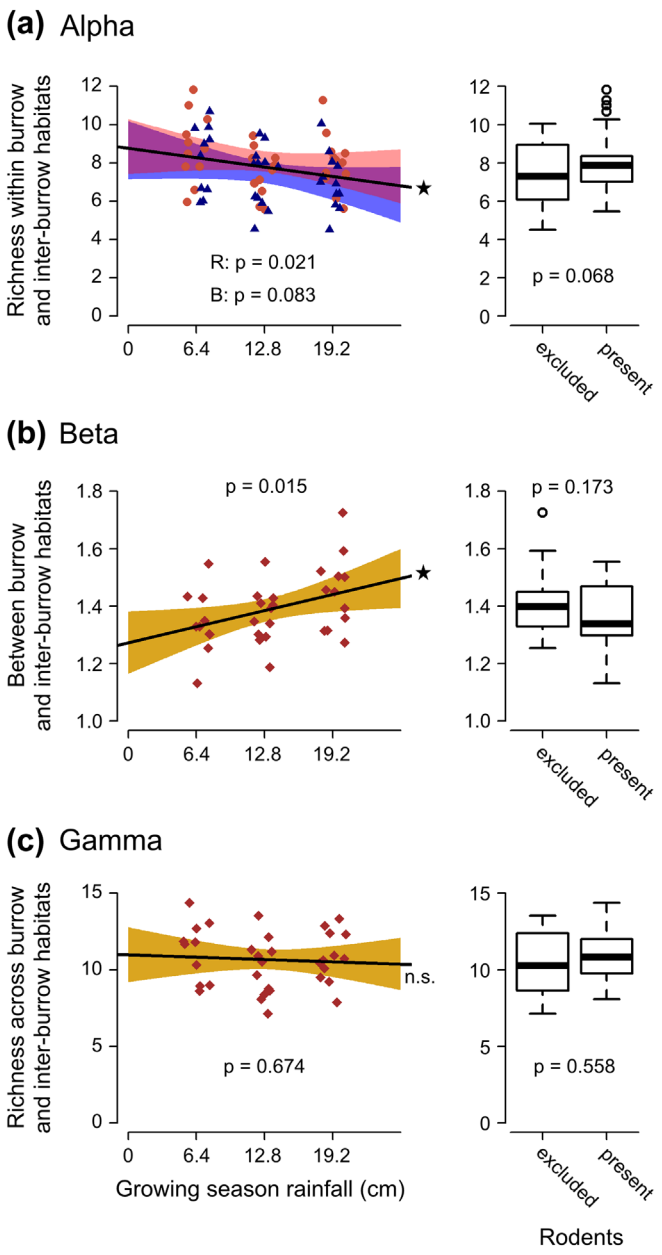

Figure 2. Plant (a) alpha, (b) beta and (c) gamma diversity responses to rainfall and rodent presence manipulations. p-values provided are from linear mixed effects models. Rainfall effects are visualized by post hoc regressions with 95% confidence intervals, while rodent presence effects are shown as boxplots. Significant post hoc regressions (slope: $p \leq 0.05$) are indicated by stars. Confidence intervals are shown for each habitat in (a). Points depict plot-level data and are jittered to show variability along the y-axis. The effect of rodent burrowing is shown in (a), but is not included in (b) and (c) because these diversity measures were calculated across burrow and inter-burrow habitats. Beta diversity was estimated using paired alpha diversity measures (burrow versus inter-burrow) to explicitly represent turnover between habitats within each plot.

Table 1. Plant species list and relative cover off and on burrows, averaged across sites and other experimental factors. Species in bold were included in the multivariate analyses. Most species have annual life histories and are native to California; perennial (p) and exotic (e) plants are designated following species names. Significant indicator species ($p \leq 0.05$) are shown with '*' off or on burrow and with the corresponding rainfall treatment (↓: 6.4, →: 12.8, ↑: 19.2 cm).

Plant ID	Scientific name	Family	Off burrow	On burrow
Forbs				
F1	*Allium* sp. (p)	Alliaceae	0.0001	0.0000
F2	*Amsinckia menziesii*	Boraginaceae	0.0001	0.0000
F3	***Amsinckia tessellata***	**Boraginaceae**	**0.0173**	**0.0690**
F4	***Calandrinia menziesii***	**Montiaceae**	**0.0110**	**0.0088**
F5	*Camissonia campestris*	Onagraceae	0.0001	0.0000
F6	***Capsella bursa-pastoris* (e)**	**Brassicaceae**	**0.0005**	**0.0004**
F7	*Castelleja exserta*	Orobanchaceae	0.0000	0.0001
F8	***Caulanthus lasiophyllus***	**Brassicaceae**	**0.0291**	**0.0473**
F9	***Chorizanthe uniaristata***	**Polygonaceae**	**0.0034**	**0.0001**
F10	*Croton setiger*	Euphorbiaceae	0.0000	0.0001
F11	*Descurainia sophia* (e)	Brassicaceae	0.0005	0.0001
F12	***Dichelostemma capitatum* (p)**	**Themidaceae**	**0.0027**	**0.0008**
F13	***Eriogonum gracillimum***	**Polygonaceae**	**0.0021**	**0.0056**
F14	***Erodium cicutarium* (e)**	**Geraniaceae**	**0.3299**	**0.3288**
F15	***Herniaria hirsuta* ssp. *cineria* (e)**	**Caryophyllaceae**	**0.0173**	**0.0109**
F16	***Hollisteria lanata***	**Polygonaceae**	**0.0060**	**0.0036**
F17	***Lasthenia californica***	**Asteraceae**	**0.0219**	**0.0084**
F18	***Lasthenia minor***	**Asteraceae**	**0.0248**	**0.0192**
F19	***Lepidium dictyotum***	**Brassicaceae**	**0.0049**	**0.0091**
F20	***Lepidium nitidum***	**Brassicaceae**	**0.1835**	**0.1124**
F21	***Leptosiphon liniflorus***	**Polemoniaceae**	**0.0018 *↑**	**0.0000**
F22	***Malacothrix coulteri***	**Asteraceae**	**0.0015**	**0.0021**
F23	*Microseris douglasii*	Asteraceae	0.0003	0.0000
F24	***Microseris elegans***	**Asteraceae**	**0.0003**	**0.0006**
F25	***Monolopia lanceolata***	**Asteraceae**	**0.0005**	**0.0012**
F26	***Pectocarya penicillata***	**Boraginaceae**	**0.0151**	**0.0030**
F27	*Plagiobothrys canescens*	Boraginaceae	0.0000	0.0001
F28	*Plantago erecta*	Plantaginaceae	0.0000	0.0001
F29	***Salsola tragus* (e)**	**Chenopodiaceae**	**0.0003**	**0.0001**
F30	*Sisymbrium altissimum* (e)	Brassicaceae	0.0003	0.0000
F31	***Sisymbrium irio* (e)**	**Brassicaceae**	**0.0019**	**0.0014**
F32	***Trichostema lanceolatum***	**Lamiaceae**	**0.0012 *↑**	**0.0000**
F33	***Tropidocarpum gracile***	**Brassicaceae**	**0.0229**	**0.0121**
		Total forbs	0.7016	0.6467
Grasses				
G1	***Bromus madritensis* ssp. *rubens* (e)**	**Poaceae**	**0.0200**	**0.0308**
G2	***Festuca bromoides* (e)**	**Poaceae**	**0.0044**	**0.0030**
G3	***Festuca microstachys* v. *pauciflora***	**Poaceae**	**0.0246 *→**	**0.0221**
G4	***Festuca myuros* v. *hirsuta* (e)**	**Poaceae**	**0.0018**	**0.0008**
G5	***Hordeum murinum* (e)**	**Poaceae**	**0.0505**	**0.1399 *↑**
G6	*Poa secunda* ssp. *secunda* (p)	Poaceae	0.0004	0.0000
G7	***Schismus arabicus* (e)**	**Poaceae**	**0.1889**	**0.1536**
		Total grasses	0.2905	0.3502
Legumes				
L1	***Acmispon wrangelianus***	**Fabaceae**	**0.0022**	**0.0016 *↓**
L2	***Astragalus* sp.**	**Fabaceae**	**0.0023**	**0.0001**
L3	***Lupinus microcarpus* v. *microcarpus***	**Fabaceae**	**0.0010**	**0.0001**
L4	***Trifolium gracilentum***	**Fabaceae**	**0.0025**	**0.0012**
		Total legumes	0.0080	0.0032

$p = 0.001$; Fig. 3d); the cline in the opposite direction aligns with communities off burrows. Vectors representing correlations with soil properties are included in Fig. 3d, which show that the compositional change due to burrowing and its corresponding rainfall cline covaried with N mineralization, the dominant soil property in the NMDS (according to R^2 values, Supplementary material Appendix 1 Table A6). Burrowing did not affect multivariate dispersion (Fig. 3g, Supplementary material Appendix 1 Table A5). The lack of an interactive effect between rodent presence and rainfall

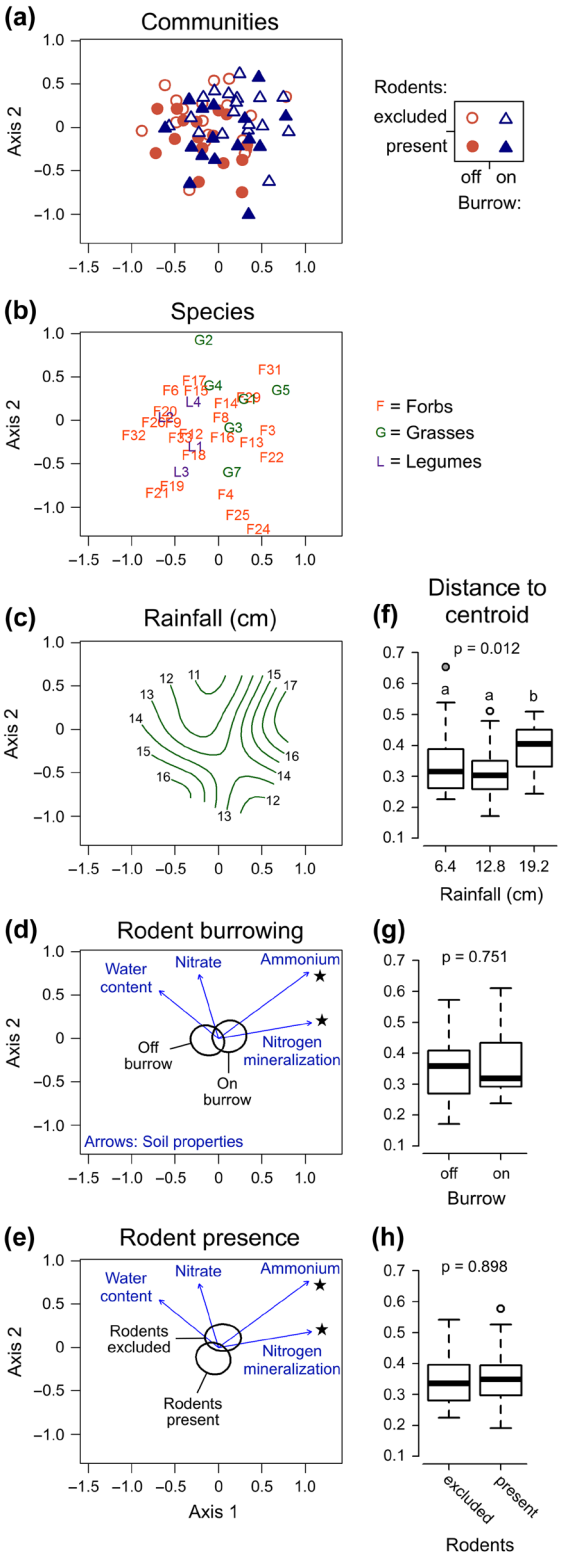

Figure 3. Nonmetric multidimensional scaling (NMDS) ordination of plant community composition (a–e) and dispersion (f–h) relationships with rainfall, rodent burrowing, and rodent presence. (a) Individual communities illustrate Bray–Curtis dissimilarities based on plot-level data. (b) Position of individual plant species in multivariate space; codes match species nomenclature in Table 1. (c) Contours for the effect of rainfall on community composition. (d) Ellipses (99% SE) for the effect of burrowing on community composition. (e) Ellipses (99% SE) for the effect of rodent presence on community composition. Vectors for soil properties (arrows) are also included in (d) and (e), and of these, nitrogen mineralization and ammonium content had significant fit within the NMDS (stars indicate $p < 0.05$). Community dispersion measured as the distance to multivariate centroids is shown as boxplots across (f) rainfall levels, (g) on and off burrows and (h) when rodents were present or excluded. p-values in (f–h) are from permutational tests (PERMDISP). Letters above boxplots in (f) indicate significant ($p \leq 0.05$) Tukey's post hoc differences (excluding the extreme outlying data point in gray). NMDS stress was 0.214.

or burrowing indicates that the presence of rodents did not alter the above results (Supplementary material Appendix 1 Table A4). Rodent presence did impact the average community composition (Fig. 3e), but had no effect on dispersion (Fig. 3h, Supplementary material Appendix 1 Table A5).

To understand the contribution of individual species to community change, we used indicator species analyses to identify plants that represented communities on and off burrows under the different rainfall conditions. Significant indicator species are summarized in Table 1 (indicator values for all species are in Supplementary material Appendix 1 Table A7). Five species were identified as significant indicators, of which three were representative of high rainfall conditions. The exotic grass *Hordeum murinum* had the highest indicator value and was indicative of communities on burrows at high rainfall, whereas the native forbs *Leptosiphon liniflorus* and *Trichostema lanceolatum* were representative of assemblages off burrows under high rainfall. The influence of these species on community composition can be seen in the NMDS (Fig. 3b). The position of *H. murinum* (G5) corresponds to the increasing rainfall cline associated with burrows, while the positions of *L. liniflorus* (F21) and *T. lanceolatum* (F32) correspond with the rainfall cline in the opposite direction, which is associated with habitat off burrows.

Discussion

Our study demonstrates that ecosystem engineering causes different amounts of non-structural abiotic change across an environmental gradient, despite no differences in structural change. Furthermore, these non-structural properties were abiotic resources for plants, and changes in resource availability influenced species diversity responses to ecosystem engineering. Our results support the hypothesis that the capacity for ecosystem engineering to cause non-structural abiotic change and concomitant biodiversity responses is determined by the position of a local environment on environmental gradients and is independent of the magnitude of structural change due to engineering. In support of this conclusion, the rodent exclosure treatment showed that soil and plant responses to burrowing and rainfall were insensitive to the

presence of the engineer species and burrow maintenance, even after excluding kangaroo rats for eight years. These results suggest that long-lasting ecosystem engineering may have effects on biodiversity that are particularly dependent on the position of communities along environmental gradients. Accounting for the potential for engineering to alter non-structural abiotic conditions may be important for predicting biodiversity responses when engineered structures are stable through space and time.

In our grassland study system, rainfall-driven change in soil resources due to engineering resulted in increased species turnover between engineered and non-engineered habitats, which stabilized landscape-level richness. Without burrowing, gamma diversity would have decreased due to greater species dominance in response to higher rainfall, similar to alpha diversity in the inter-burrow habitat. Though additional study is needed, we anticipate that such biodiversity patterns may be common in response to engineering-created heterogeneity, as long as functionally-diverse species are present during community assembly. While not explicitly studied here, the regional species pool from which ecological communities assemble is also important for understanding biodiversity responses to ecosystem engineering. A functionally diverse species pool, including habitat specialists, is needed for species diversity to respond to environmental heterogeneity (Questad and Foster 2008, Myers and Harms 2009). In our investigation, the regional species pool had enough functional diversity for communities to become more dissimilar with higher rainfall. Consideration of functional traits may be a fruitful way forward for understanding the mechanisms governing species diversity responses to engineering-induced changes in non-structural abiotic resources.

Of the soil properties we investigated, our results suggest that increased species turnover corresponded with greater differences in net N mineralization between engineered and non-engineered habitats. Off burrows, N mineralization was indistinguishable from zero across the precipitation gradient, whereas on burrows, this N cycling rate increased with rainfall. These results are consistent with previous studies that have found N mineralization to be greater on banner-tailed kangaroo rat burrows than inter-burrow areas (Moorhead et al. 1988) and N pools to be greater on versus off kangaroo rat burrows (Greene and Reynard 1932, Moorhead et al. 1988, Mun and Whitford 1990, Gurney et al. 2015). We observed that the nitrate pool diminished with greater rainfall, likely a result of the increase in primary production with rainfall. Altogether, these results indicate that with higher rainfall, burrows are able to maintain higher mineralization rates compared to off burrow habitat. Future research to detect differences in inorganic N pools should consider more integrative measurements, such as ion exchange resin bags. Furthermore, plant traits linked to N acquisition are likely to be important for understanding biodiversity responses in this system.

While ecosystem engineering increases niche opportunities that result in greater native diversity, increased niche space also provides opportunities for invasive species establishment (Shea and Chesson 2002). Increased N availability on burrows may facilitate the establishment of nitrophilous exotic grasses, such as *H. murinum* and *Bromus madritensis* ssp. *rubens* (Brooks 2003, DeFalco et al. 2003, Going et al. 2009). Especially where *H. murinum* became abundant, the patterns of diversity that we observed are likely influenced by competitive exclusion (MacArthur and Levins 1967, Levine and HilleRisLambers 2009). *Hordeum murinum* and other exotic grass species can displace native plants at local scales in California grasslands (DiVittorio et al. 2007, HilleRisLambers et al. 2010), and the facilitative effect of burrowing on such invasions may lead to a decline in landscape-level diversity over time (Schiffman 1994). Burrows are important habitat for native species, such as the forbs *Amsinckia tessellata* and *Caulanthus lasiophyllus* (Grinath et al. 2018), and their abundances may be particularly prone to decline during rainy periods. These dynamics may be kept in check by climate change, as the region is expected to become more arid in the coming century (Seager et al. 2007, Cayan et al. 2008). Moreover, *H. murinum* and other large-seeded invasive grasses (ex. *Bromus madritensis* ssp. *rubens*) are important food sources for the federally endangered giant kangaroo rat (Schiffman 1994, Gurney et al. 2015), and kangaroo rat foraging can offset the facilitative effects of burrowing on these grasses (Grinath et al. 2018). Indeed, the results presented here indicate that effects of rodent presence on soils and plants are frequently opposite those of rodent burrowing (Fig. 1c, 2a). While the current study shows that kangaroo rat burrowing maintains landscape-level diversity by facilitating an exotic species, it is unclear whether this effect is ultimately detrimental or beneficial for native plant species that benefit from burrow habitat during drier periods. Further study is needed to understand feedback dynamics between exotic plant species and giant kangaroo rats and to anticipate how changes in giant kangaroo rat populations and burrowing will affect plant diversity in the future.

Our study may shed light on an ongoing debate concerning facilitative interactions across environmental stress gradients. The stress gradient hypothesis posits that facilitative interactions become more frequent as environments become more stressful (Bertness and Callaway 1994). While much evidence supports the stress gradient hypothesis, there are also many exceptions (Maestre et al. 2005, 2006, 2009, Lortie and Callaway 2006, Holmgren and Scheffer 2010, He et al. 2013, He and Bertness 2014). The hypothesis has primarily been tested in the contexts of plant–plant interactions and of pairwise interactions, but it has been increasingly applied in other contexts including interactions with animals and dynamics at the community-level (Soliveres et al. 2015). Perhaps some of the different results arising from these different contexts can be commonly understood by considering how ecosystem engineering results in facilitation along environmental gradients.

For example, Wright et al. (2006) studied how ecosystem engineering by shrubs increased landscape-level plant diversity in an arid ecosystem. In that system, the positive effect of shrubs on diversity decreased as precipitation increased,

indicating that facilitation was more frequent under stressful drought conditions (Wright et al. 2006). In contrast, we found that gamma diversity did not change as precipitation increased because ecosystem engineering by kangaroo rats had a greater positive effect on beta diversity, indicating that burrowing had more facilitative effects on plants when drought stress was alleviated. We suggest that these differences could be reconciled by considering the potential for non-structural abiotic change due to the two types of engineering. Shrubs benefit other plants by increasing soil moisture (Wright et al. 2006) and have stronger effects on soils and plants under drought conditions, when there is greater capacity for shrubs to alter soil conditions relative to surrounding habitats. Even though the structural effects of shrubs likely intensified with higher rainfall (due to shrub growth), their facilitative effects could weaken because there is little difference in soil moisture between shrub-engineered and non-engineered habitats (i.e. soil moisture cannot increase if soils are saturated). Likewise, burrow engineering by kangaroo rats also had stronger effects on soils and plants when there was a greater capacity for change in abiotic properties. However, counter to engineering by shrubs, this occurred in the opposite direction across the rainfall gradient because burrowing decreases soil moisture (i.e. soil moisture cannot decrease if there is no moisture present). Though shrubs and kangaroo rats are vastly different organisms, their ecosystem engineering effects occur via a common medium (soils) and abiotic properties (ex. soil moisture), and the same principles may be applicable in both contexts. Further consideration of the potential for engineering to cause changes in the non-structural abiotic environment may be warranted to aid our understanding of facilitation across environmental gradients.

Human activities are altering climate and ecosystems from local to global scales (Vitousek et al. 1997), with grave consequences for biodiversity (Ceballos et al. 2017). While ecosystem management and restoration are beginning to embrace ecosystem engineering as an important process for maintaining biodiversity (Byers et al. 2006), we still have much to learn. Efforts to conserve Earth's rapidly declining biodiversity may hinge on understanding how ecosystem engineering and environmental gradients interact to create habitat conditions in which diverse communities can persist.

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References

Anderson, M. J. and Walsh, D. C. I. 2013. PERMANOVA, ANOSIM and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? – Ecol. Monogr. 83: 557–574.

Anderson, M. J. et al. 2006. Multivariate dispersion as a measure of beta diversity. – Ecol. Lett. 9: 683–693.

Anderson, M. J. et al. 2011. Navigating the multiple meanings of ß diversity: a roadmap for the practicing ecologist. – Ecol. Lett. 14: 19–28.

Bean, W. T. et al. 2014. A multi-scale distribution model for non-equilibrium populations suggests resource limitation in an endangered rodent. – PLoS One 9: e106638.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. – Trends Ecol. Evol. 9: 191–193.

Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. – J. Appl. Ecol. 40: 344–353.

Bulleri, F. et al. 2016. Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. – Funct. Ecol. 30: 70–78.

Byers, J. E. et al. 2006. Using ecosystem engineers to restore ecological systems. – Trends Ecol. Evol. 21: 493–500.

Cavieres, L. A. and Badano, E. I. 2009. Do facilitative interactions increase species richness at the entire community level? – J. Ecol. 97: 1181–1191.

Cayan, D. R. et al. 2008. Climate change scenarios for the California region. – Clim. Change 87: S21–S42.

Ceballos, G. et al. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. – Proc. Natl Acad. Sci. USA 114: E6089–E6096.

Cooper, L. D. and Randall, J. A. 2007. Seasonal changes in home ranges of the giant kangaroo rat (*Dipodomys ingens*): a study of flexible social structure. – J. Mammal. 88: 1000–1008.

DeFalco, L. A. et al. 2003. Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* ssp. *rubens* (Poaceae) and two native species. – Am. J. Bot. 90: 1045–1053.

DiVittorio, C. T. et al. 2007. Spatial and temporal patterns of seed dispersal: an important determinant of grassland invasion. – Ecol. Appl. 17: 311–316.

Dufrene, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. – Ecol. Monogr. 67: 345–366.

Going, B. M. et al. 2009. Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. – Oecologia 159: 839–847.

Gotelli, N. J. and Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. – Ecol. Lett. 4: 379–391.

Greene, R. A. and Reynard, C. 1932. The influence of two burrowing rodents, *Dipodomys spectabilis spectabilis* (kangaroo rat) and *Neotoma albigula albigula* (pack rat) on desert soils in Arizona. – Ecology 13: 73–80.

Grinath, J. B. et al. 2018. Animals alter precipitation legacies: trophic and ecosystem engineering effects on plant community temporal dynamics. – J. Ecol. 106: 1454–1469.

Grinath, J. B. et al. 2019. Data from: Environmental gradients determine the potential for ecosystem engineering effects. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.gk1r3s5>.

Grinnell, J. 1932. Habitat relations of the giant kangaroo rat. – J. Mammal. 13: 305–320.
Gurney, C. M. et al. 2015. Restoration of native plants is reduced by rodent-caused soil disturbance and seed removal. – Rangeland Ecol. Manage. 68: 359–366.
Hastings, A. et al. 2007. Ecosystem engineering in space and time. – Ecol. Lett. 10: 153–164.
He, M. and Dijkstra, F. A. 2014. Drought effect on plant nitrogen and phosphorus: a meta-analysis. – New Phytol. 204: 924–931.
He, Q. and Bertness, M. D. 2014. Extreme stresses, niches and positive species interactions along stress gradients. – Ecology 95: 1437–1443.
He, Q. et al. 2013. Global shifts towards positive species interactions with increasing environmental stress. – Ecol. Lett. 16: 695–706.
HilleRisLambers, J. et al. 2010. California annual grass invaders: the drivers or passengers of change? – J. Ecol. 98: 1147–1156.
Holmgren, M. and Scheffer, M. 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. – J. Ecol. 98: 1269–1275.
Jones, C. G. et al. 1994. Organisms as ecosystem engineers. – Oikos 69: 373–386.
Jones, C. G. et al. 1997. Positive and negative effects of organisms as physical ecosystem engineers. – Ecology 78: 1946–1957.
Jones, C. G. et al. 2010. A framework for understanding physical ecosystem engineering by organisms. – Oikos 119: 1862–1869.
Levin, S. A. 1974. Dispersion and population interactions. – Am. Nat. 108: 207–228.
Levine, J. M. and HilleRisLambers, J. 2009. The importance of niches for the maintenance of species diversity. – Nature 461: 254–257.
Lortie, C. J. and Callaway, R. M. 2006. Re-analysis of meta-analysis: support for the stress–gradient hypothesis. – J. Ecol. 94: 7–16.
MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. – Am. Nat. 101: 377–385.
Madrigal, J. et al. 2011. Bottom-up control of consumers leads to top–down indirect facilitation of invasive annual herbs in semiarid Chile. – Ecology 92: 282–288.
Maestre, F. T. et al. 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. – J. Ecol. 93: 748–757.
Maestre, F. T. et al. 2006. The stress–gradient hypothesis does not fit all relationships between plant–plant interactions and abiotic stress: further insights from arid environments. – J. Ecol 94: 17–22.
Maestre, F. T. et al. 2009. Refining the stress–gradient hypothesis for competition and facilitation in plant communities. – J. Ecol. 97: 199–205.
McIntire, E. J. B. and Fajardo, A. 2014. Facilitation as a ubiquitous driver of biodiversity. – New Phytol. 201: 403–416.
Meserve, P. L. et al. 2003. Thirteen years of shifting top–down and bottom–up control. – BioScience 53: 633–646.
Moorhead, D. L. et al. 1988. Cover of spring annuals on nitrogen-rich kangaroo rat mounds in a Chihuahuan Desert grassland. – Am. Midl. Nat. 120: 443–447.
Mun, H.-T. and Whitford, W. G. 1990. Factors affecting annual plants assemblages on banner-tailed kangaroo rat mounds. – J. Arid Environ. 18: 165–173.
Myers, J. A. and Harms, K. E. 2009. Seed arrival, ecological filters and plant species richness: a meta-analysis. – Ecol. Lett. 12: 1250–1260.
Prugh, L. R. and Brashares, J. S. 2012. Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. – J. Anim. Ecol. 81: 667–678.
Questad, E. J. and Foster, B. L. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. – Ecol. Lett. 11: 717–726.
Rankine, W. J. M. 1853. On the general law of the transformation of energy. – Proc. Phil. Soc. Glasgow 3: 276–280.
Robertson, G. P. et al. (eds) 1999. Standard soil methods for long-term ecological research. – Oxford Univ. Press.
Romero, G. Q. et al. 2015. Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. – Biol. Rev. 90: 877–890.
Schiffman, P. M. 1994. Promotion of exotic weed establishment by endangered giant kangaroo rats (*Dipodomys ingens*) in a California grassland. – Biodivers. Conserv. 3: 524–537.
Schob, C. et al. 2013. Variability in functional traits mediates plant interactions along stress gradients. – J. Ecol. 101: 753–762.
Seager, R. et al. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. – Science 316: 1181–1184.
Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. – Trends Ecol. Evol. 17: 170–176.
Soliveres, S. et al. 2015. Moving forward on facilitation research: response to changing environments and effects on diversity, functioning and evolution of plant communities. – Biol. Rev. 90: 297–313.
Vitousek, P. M. et al. 1997. Human domination of Earth's ecosystems. – Science 277: 494–499.
Whitford, W. G. and Kay, F. R. 1999. Biopedturbation by mammals in deserts: a review. – J. Arid Environ. 41: 203–230.
Whittaker, R. H. 1972. Evolution and measurement of species diversity. – Taxon 21: 213–251.
Williams, D. F. and Kilburn, K. S. 1991. Dipodomys ingens. – Mamm. Spec. 377: 1–7.
Wright, J. P. and Jones, C. G. 2004. Predicting effects of ecosystem engineers on patch-scale species richness from primary production. – Ecology 85: 2071–2081.
Wright, J. P. et al. 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. – J. Ecol. 94: 815–824.
Yahdjian, L. and Sala, O. E. 2002. A rainout shelter design for intercepting different amounts of rainfall. – Oecologia 133: 95–101.
Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.

Supplementary material (available online as Appendix oik-05768 at <www.oikosjournal.org/appendix/oik-05768>). Appendix 1.