




ARTICLE

Climate mediates long-term impacts of rodent exclusion on desert plant communities

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Abstract

Determining how climate affects biotic interactions can improve understanding of drivers of context-dependence and inform predictions of how interactions may influence plants under future climates. In arid environments, the community-level impacts of seed predators may depend strongly on aridity; yet, long-term studies documenting impacts of granivores on plant communities over variable climate conditions remain scarce. We evaluated how rodent exclusion interacted with climate to influence grassland and shrubland forb communities and the community-scale distribution of seed mass over 15 years in the climatically variable northern Chihuahuan Desert. In this dynamic system, two seasonally distinct plant community phases occur annually, one in spring and the other during the summer monsoon. Rodent exclusion significantly altered the community composition of monsoon season plant communities in both grassland and shrubland, but did not affect spring plant composition. Rodents suppressed the abundance of larger-seeded forb species and promoted smaller-seeded species. As a consequence, rodent exclusion increased community seed mass (CWM) in monsoon forb communities, most strongly in grassland. The magnitude of impacts of rodents on seed mass varied substantially from year-to-year, tracking variation in climate. Specifically, rodent exclusion increased community mean seed mass the most in dry years (grassland) or in years following dry years (shrubland). Rodent exclusion had relatively weak effects on plant species diversity and richness. Our results indicate that climate interacts with the presence of rodents to structure not only the composition but also the traits of desert plant communities.

KEYWORDS

Chihuahuan Desert, community-weighted mean, plant communities, post-dispersal seed predation, precipitation, rodents, seed size

INTRODUCTION

The long-term effects of post-dispersal seed predation on plant communities remain surprisingly enigmatic. On the one hand, we know that these consumers have great

potential to affect community composition as post-dispersal seed predation causes extensive seed loss. Seed consumption rates by granivorous rodents can often be high (Crawley, 1992; Orrock et al., 2006), even greater than pre-dispersal seed loss (Hulme, 2002; Moles et al., 2003), and

plants cannot compensate for these losses. When seeds of single species have been added to plots where consumer access has been manipulated, post-dispersal seed loss commonly can strongly suppress seedling recruitment (Albert et al., 2005; Bricker et al., 2010; Ferreira et al., 2011; Hulme, 1994; Longland, 2007; Orrock et al., 2008). On the other hand, fewer of these types of studies have been performed at the plant community level. Instead, most “community assembly” studies focus on interspecific plant competition as a filter affecting species composition and trait distributions (Funk et al., 2017; Lavorel et al., 2013), ignoring the influences of generalist seed consumers (Larios et al., 2017). But where community-level studies have manipulated rodent access to seeds, researchers have found that seed predation can bias seedling recruitment against native plant species in favor of exotic species (Connolly et al., 2014; Lucero & Callaway, 2018; Maron et al., 2012; Pearson et al., 2011; Pearson, Icasatti, et al., 2014; Pearson, Hierro, et al., 2014) and favor large-over small-seeded species in open habitats (Dylewski et al., 2020; Maron et al., 2012, 2018; Mittlebach & Gross, 1984; Moyano et al., 2019; Reader, 1993). However, owing to their relatively short duration, these studies do not reveal how rodent seed predation influences longer-term (>5 years) patterns of plant community structure that depend not only on recruitment but also other plant life-history transitions.

One of the most iconic long-term experiments evaluating the impacts of rodents upon an intact community has been the work by Jim Brown and colleagues in the Chihuahuan Desert in Arizona. Exclusion of rodents from large plots for >22 years transformed the plant community from one dominated by short-statured, small-seeded annual grasses to one dominated by large-seeded, large-statured grasses and forbs (Brown & Heske, 1990; Curtin et al., 1999; Guo et al., 1995; Inouye et al., 1980; Samson et al., 1992). These changes resulted from a combination of reduced seed predation and reduced disturbance, caused mainly by the foraging and burrowing activities of kangaroo rats (*Dipodomys* spp.) (Brown & Heske, 1990). High-frequency disturbances by kangaroo rats have similarly been shown to influence plant communities in California (Prugh & Brashares, 2012). Surprisingly, outside of this work, we are unaware of any experimental studies longer than five years that have examined how the exclusion of an entire rodent community influences an intact plant community (see Gutiérrez et al. [1999]; Meserve et al. [2003] for effects of one rodent species and Davidson et al. [2010] for rodents and domestic cattle). As a result, the extent to which rodents have long-term, sustained impacts on plant communities remains uncertain.

The uncertainty of predictions on the community-level effects of rodents derives, in part, from how seed predation interacts with interannual variation in abiotic conditions to influence long-term plant community structure. Increasingly large interannual variation is a common feature of ongoing climate change as well as future climate projections (Maurer et al., 2020) and is likely a fundamental, although understudied, factor shaping plant community assembly (Angert et al., 2009; Gherardi & Sala, 2015). Evaluating how climate shifts the strength of biotic interactions is important, because seed predators might influence plant recruitment only in years when consumers are abundant and/or abiotic conditions are favorable for plant recruitment (Brown & Ernest, 2002; Meserve et al., 2003). When environmental conditions, such as drought, limit plant recruitment, seed predation may not have large impacts on plant community composition because seed loss is decoupled from subsequent recruitment. Alternatively, dry conditions may promote stronger top-down effects of seed predation than that occur in wet years, because the smaller pool of plant resources amplifies the effect size of consumers on plants.

The biotic–abiotic interactions driving community change are of particular relevance in dryland communities that experience strong seasonal and annual variations in rainfall. For example, the climate in North American drylands is strongly driven by cyclic influences of the El Niño–Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (Verdon & Franks, 2006). Large swings in the timing and amount of rainfall greatly influence plant productivity (Brown & Ernest, 2002; Collins et al., 2020; Maurer et al., 2020; Muldavin et al., 2008; Rudgers et al., 2018) and alter plant community composition through species-specific patterns of germination out of the seedbank (e.g., Angert et al., 2009). Shifts in summer versus winter precipitation amounts correlate with increases in dominant C₄ grasses (e.g., black grama, *Bouteloua eriopoda*) during La Niña events, and increased C₃ shrubs (e.g., creosotebush, *Larrea tridentata*) during El Niño events (Muldavin et al., 2008). Variable precipitation can influence rodent abundances from the bottom-up (Báez et al., 2006; Muldavin et al., 2008; Mulhouse et al., 2017), and rodent abundances correlate positively with plant production, typically with a 6–12 month time lag (Ernest et al., 2000; see also Thibault et al., 2010). For example, dominant, granivorous kangaroo rats can increase with the production of annual or perennial grasses (Lightfoot et al., 2012; Schooley et al., 2018). In the past 100 years, average aridity during the monsoon season has increased (Maurer et al., 2020; Rudgers et al., 2018) in southwestern North American drylands, which is indicative of long-term drying, despite no long-term trend in precipitation amount

(Petrie et al., 2014). Moreover, interannual variability in aridity has increased throughout the region (Maurer et al., 2020; Rudgers et al., 2018). Thus, dynamic seasonal aridity, precipitation, and plant production may cause temporal variation in the magnitude of rodents' influence on the plant community. So, the community impacts of seed predation may be strongly context-dependent, although studies examining the interaction between seed predation and spatio-temporal patterns of abiotic conditions are uncommon but see (Brown & Ernest, 2002; Lima et al., 2008; Meserve et al., 2003; Thibault et al., 2010).

To better understand how seed predators interact with variable climate conditions, we analyzed long-term vegetation data from the Sevilleta Long-Term Ecological Research (SevLTER) program in the northern Chihuahuan Desert in central New Mexico, a site that experiences high interannual variability in precipitation (Mulhouse et al., 2017; Petrie et al., 2014; Rudgers et al., 2018). Vegetation was measured for 15 years inside and outside of large-scale rodent exclosures. Analysis of pre-treatment data began in 1995 and continued to the end of the experiment in 2009. Some results from this experiment were analyzed by Báez et al. (2006), who documented strong bottom-up effects of precipitation on the plant community but few top-down effects by rodents. Here, we analyze a longer time series than Báez et al. (2006) and add new information on seed mass to address the following questions: (1) *To what extent does rodent exclusion alter plant community composition over a long time scale (e.g., 15 years for this study)?* We hypothesized that the effects of rodent exclusion should increase with time but vary among years owing to the large interannual variation in precipitation and drought (e.g., Muldavin et al., 2008; Mulhouse et al., 2017; Rudgers et al., 2018). (2) *Does rodent exclusion increase plant species diversity?* We hypothesized that if rodents preferred large-seeded species, then rodent exclusion would enhance alpha diversity and plant species richness. (3) *Do larger-seeded plant species increase under rodent exclusion, and if so, is this manifest at the community level as greater community-weighted seed mass or altered seed mass distributions?* Rodent preferences for seeds can depend on mammalian body size, population density, interspecific competition, predator avoidance, microhabitat, and soil characteristics (Hughes et al., 1994; M'Closkey, 1980; Price & Heinz, 1984; Price & Podolsky, 1989). The net effects of rodents on plants hinge on the balance among processes that include seed loss from consumption, benefits to seeds from caching and dispersal, and rodent-mediated soil disturbances creating opportunities for seedling recruitment (e.g., Longland et al., 2001; Swartz et al., 2010). Thus, selective foraging by an entire community of diverse rodent taxa involves several factors that may, or may not, bias plant community

composition toward larger-seeded plant species. Moreover, rodents could alter the shape of trait distributions through selective foraging (e.g., reducing variance, increasing skewness toward large seed sizes, and increasing kurtosis), indicating abundant plant species sharing similar trait values (Gaedke & Klauschies, 2017; Gross et al., 2017). (4) *Do the impacts of seed predation on community seed mass track interannual differences in climate?* We predicted that rodent exclusion should have the largest effects on plant communities and community traits during or after wet years, when conditions favor both annual and perennial forb production (Mulhouse et al., 2017), allowing the impacts of rodents to be manifest. These effects may lag behind wet years because rodent populations can take 6–12 months to respond to rainfall-driven increases in plant production (Ernest et al., 2000).

METHODS

Natural history

Plants

The Sevilleta National Wildlife Refuge is located at the northern edge of the Chihuahuan Desert with typical Chihuahuan Desert grasslands and shrublands (Dick-Peddie, 1993). Research sites were established within an extensive black grama grass (*Bouteloua eriopoda*) grassland (N: 34°19'59.16", S: 34°19'59.16", E: -106°44'9.6", W: -106°44'9.6") and within a distant creosotebush (*Larrea tridentata*) shrubland (N: 34°17'45.6", S: 34°17'45.6", E: -106°55'37.2", W: -106°55'37.2") with different forb taxa dominating both ecosystems in spring versus fall (Muldavin et al., 2008; Mulhouse et al., 2017).

Mammals

The ecology of granivorous desert rodent assemblages has been well-studied across North American drylands (Davidson et al., 1985; Heske et al., 1993; Hernandez et al., 2005; Kelt, 2011; Kotler & Brown, 1988; Lima et al., 2008). The Sevilleta rodent community, like other desert rodent assemblages, is dominated by heteromyid granivores that forage mostly on forb seeds, and to a lesser extent on grass seeds, leaves, and insects (Ernest et al., 2000; Hope & Parmenter, 2007; Yeakel et al., 2020). On average, rodents were ~40% more abundant in shrubland (11.7 ± 5.0 rodents/ha) than grassland (8.4 ± 1.2 rodents/ha). The most common species are *Perognathus flavus* (silky pocket mouse) in both grassland and shrubland, *Dipodomys ordii* (Ord's kangaroo rat) in the

grassland, and *Dipodomys merriami* (Merriam's kangaroo rat) in shrubland. All of these species are larger hoarders, although *D. ordii* can also scatter hoard. These species vary in body sizes and foraging microhabitats, based on seed availability and predation risk (Abramsky, 1988; Jenkins & Breck, 1998; Kotler, 1984; Munger & Brown, 1980).

Experimental design

Treatments

Each site was 1 km by 0.5 km and had four replicate, randomly located blocks (Figure 1). Each block was 96 m per side and contained two 36 m × 36 m experimental plots separated by at least 20 m. Treatments were randomly assigned within each block and included an unfenced control and a plot fenced with hardware cloth and poultry wire to exclude rodents and rabbits. Exclusion plot fences were monitored bi-monthly for any signs of digging or holes, which were immediately repaired. Trespass rodents inside exclosures were rare and it was obvious from soil disturbance. Any rodents found in fenced plots were trapped out immediately.

Data collection

All data and R scripts from this study are available as a data package through the Environmental Data Initiative (EDI) (Lightfoot & Rudgers, 2021). Within each plot, we positioned a grid of 36 sampling points at 5.8 m intervals on a 6 × 6 point grid, with a 3 m wide buffer between the grid and the plot perimeter. A permanent 1 m × 1 m vegetation quadrat was located at each of the 36 grid points. Percentage cover of each plant species was measured in each quadrat using a portable PVC frame partitioned into a grid of 100 squares using string. We assessed plant cover in spring (May) and in fall at peak monsoon (September) by counting the number of 10 cm squares or portions thereof (to 0.1 of a 10 cm square) occupied by each plant species. Live and dead cover was recorded separately. Here, we used only live cover for analysis. At the same time that plants were measured, soil surface disturbances also were measured directly under the string grid to the nearest value (in cm²) and the depth was measured to the nearest value (in cm). Soil surface disturbances were categorized as generated by arthropods (ant nests, spider burrows, etc.), lizards, snake tracks, rodent digging (cache digging or burrows), large mammals (pronghorn hoof impacts, deer, coyote, etc.),

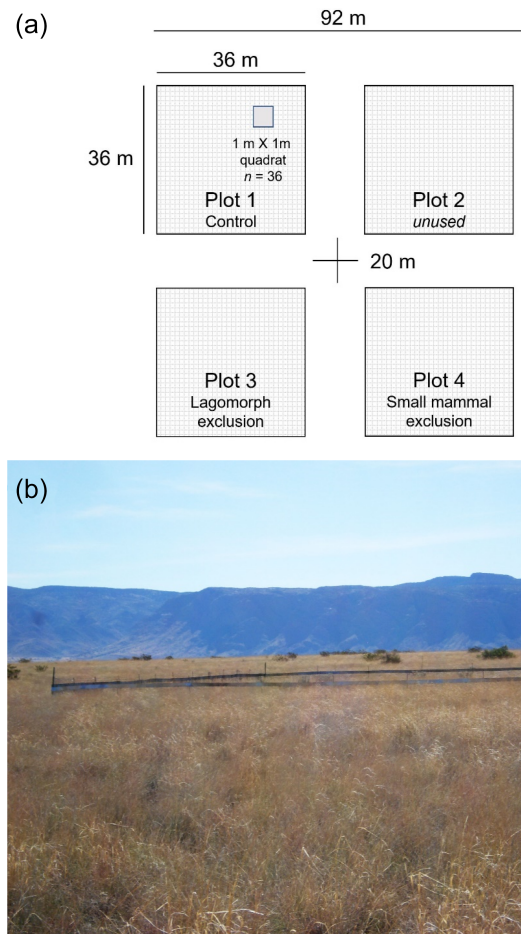


FIGURE 1 (a) Diagram of one block of the Small Mammal Exclusion Experiment design. (b) Photograph of a grassland rodent exclusion plot, credit Amaris Swann

and human caused (very rare; researchers avoided stepping on measurement quadrats).

Seed size

We measured seed mass for 5–15 mature individuals per plant species, depending on the species availability. We randomly selected healthy, mature individuals during 2017–2019, and spread effort over a broad geographical area. We weighed the mass of 5–50 air-dried seeds per individual plant, depending on seed mass and production. Intraspecific variation in seed size (mean CV = 0.21) was dwarfed by variation between species (CV = 0.96).

Climate data

Long-term meteorological stations were located at each site (see also Rudgers et al., 2018) to measure climate

variables, such as air and soil temperature, soil moisture, relative humidity, precipitation, solar radiation, and wind speed and direction. Seasonal climate data for spring spanned from October 1 to March 31 and for monsoon from April 1 to September 30. Annual climate data for spring ended March 31 and for monsoon ended 30 September, corresponding to the water year (October 1–September 30). Following Rudgers et al. (2018), we gap-filled missing daily data using data collected from the geographically nearest station within the Sevilleta National Wildlife Refuge and maintained by the SevLTER program. We calculated the Standardized Precipitation Evaporation Index (SPEI) as an integrative measure of aridity that accounts for both precipitation and temperature (Vicente-Serrano et al., 2010).

Data analyses

(1) *To what extent does rodent exclusion alter plant community composition over a long time scale?* For each sampling date, we determined the average percentage cover of each plant species across the 36 quadrats per plot. The full matrix included 16 plots, 27 sampling dates, and 118 plant species. Following standard practices for distance-based analyses, we removed observations in which a plot lacked live plant cover, which included 45 observations in spring and 19 in monsoon, of 432 total observations. We removed pre-treatment baseline data (1995) in the temporal analysis of treatment effects. One plot at the grassland site (G1R2) had a single forb species present in spring 1999 (*Lesquerella fendleri*) and was excluded from the analysis of focal species composition for that year, owing to its strong outlier status in non-metric multidimensional scaling (NMDS) space. Mean richness in the grassland during spring 1999 was 2.5 species. Additionally, in the present analysis and the analyses to follow, we removed creosotebush in shrubland and grasses from the grassland to focus on the subset of the plant community preferred by rodents (Ernest et al., 2000; Hope & Parmenter, 2007; Yeakel et al., 2020). Results from analysis of the whole plant community (Appendix S1: Table S1) included significant rodent exclusion effects on composition during the monsoon season in both grassland and shrubland (perMANOVA; Appendix S1: Table S1) and exclusion \times year interactions for plant species richness in both seasons and ecosystems and diversity in all but spring grassland.

We evaluated rodent exclusion effects on plant composition using PERMANOVA in Primer version 6.0 with a Bray–Curtis distance metric on plant cover as the measure of species abundance (Clarke & Gorley, 2009). The initial model included the fixed effects of year, site, season, treatment, and

all possible interactions among them except for season \times year because sampling ended in spring 2009. The model included the random, repeated effect of the block (nested in site) and plot (nested in site \times treatment \times block). All analyses used 10,000 permutations with Type III SS under a reduced model. The initial model revealed strong divergence in community composition between sites ($p < 0.0001$) and seasons ($p < 0.0001$). Therefore, we split the dataset into four site \times season combinations and tested for treatment \times year effects within each, including the repeated, random effect of the block. To visualize treatment effects on community composition, we used NMDS analysis on the Bray–Curtis similarity matrix with 500 random restarts. We determined which plant species were most responsible for treatment differences in plant species composition using similarity percentage (SIMPER) analysis (Clarke & Gorley, 2009).

(2) Does rodent exclusion increase plant species diversity?

We used the matrix of plant species to calculate species richness and Shannon's diversity index (H') at the scale of 1 m \times 1 m quadrats using the vegan package in R. Then, we used multilevel mixed-effects linear models with repeated measures to test for rodent exclusion effects on these diversity metrics. Models had the fixed effects of year, season, treatment, site, all possible interactions among them, and the random effects of plot identity (nested in site and treatment) and quadrat (nested in plot) (Pinheiro et al., 2017). We evaluated three temporal autocorrelation models using the package `<nlme>` in R (Pinheiro et al., 2017; R Core Team, 2020): autoregressive 1 (AR1), autoregressive 2 (AR2), or a random intercepts model with no temporal autocorrelation. We conducted model selection using the second-order Akaike Information Criterion (AICc; Bartoń, 2013), with 2 AICc required to support the more complex variance–covariance structure.

(3) Do larger-seeded plant species increase under rodent exclusion, and if so, is this manifest at the community level as greater community-weighted seed mass or altered seed mass distributions?

(3a) *Do larger-seeded plant species increase under rodent exclusion?* For each plant species, we used model selection procedures to evaluate rodent exclusion effects and temporal autocorrelation for the site(s) and season(s) in which the species occurred, using procedures described for alpha diversity in question (2). In all models, plot was included as a repeated, random effect nested within block and the treatment \times site interaction. Models using AR2 for temporal autocorrelation typically fit best for plant species present in both spring and monsoon because abundance was more strongly associated with the prior year of the same season rather than the prior season of the same year. In all models, plant species cover was log-transformed to meet assumptions of normality of residuals and homogeneity of variances.

From the best model for each plant species, we calculated the relative interaction intensity (*RII*) as a metric of effect size (Armas et al., 2004). The value of *RII* was determined from back-transformed mean percentage cover estimated using maximum likelihood (Lenth et al., 2018) as $(\text{Mean}_{\text{exclusion}} - \text{Mean}_{\text{control}}) / (\text{Mean}_{\text{control}} + \text{Mean}_{\text{exclusion}})$ such that species that increased under rodent exclusion had a positive *RII*. We did not analyze the cover of plant species with <0.1% average cover over the time series. These data were zero-inflated and failed to meet model assumptions. We determined the standard deviation of *RII* following Armas et al. (2004). For all but eight species, the year \times treatment interaction was statistically significant ($p < 0.05$), reflecting the large interannual variability. Therefore, for each species, we determined the *RII* during the year with the strongest treatment effect as well as the average *RII* over the full-time series. To examine whether plant species responses to exclusion were predicted based on seed mass, we merged the dataset of *RII* effect sizes with average plant species seed mass data to test and get the answer of the question, “Do larger-seeded plant species increase under rodent exclusion?” The model for each site was $\text{RII} \sim \text{seed mass}$, with each plant species as a unit of observation. We ran two analyses: first, using the *RII* from the year in which the exclusion treatment had the strongest effect on the species as a *least conservative* evaluation of our hypothesis; and second, using average *RII* over all sampling dates as a *most conservative* evaluation of our hypothesis.

(3b) *Do rodent exclusion effects on individual plant species increase community-weighted seed mass or alter the distribution of seed mass?* We calculated community-weighted mean (CWM) seed mass (hereafter, *community seed mass*) as well as weighted skewness, variance, and kurtosis for each vegetation quadrat using the `weighted.mean`, `w.kurtosis`, `w.var`, and `w.skewness` functions of `<tidyverse>` and `<Weighted.Desc.Stat>` in R (Wickham, 2017; <https://CRAN.R-project.org/package=Weighted.Desc.Stat>). We calculated CWM for the entire plant community and also for the most rodent-responsive subset, which excluded creosotebush and grasses. We used repeated measures, multilevel mixed-effects model on CWM metrics (mean, skewness, and kurtosis) with the fixed effects of year, season, treatment, site, possible interactions among them, and the random effects of plot identity (nested in site and treatment) and quadrat (nested in plot) (Pinheiro et al., 2017). As described for plant diversity in question (1), to get the value of mean seed mass, we compared models with alternative variance-covariance matrices to detect temporal autocorrelation; the best model for mean seed mass used AR2. We obtained marginal R^2 following Lefcheck (2016) and tested for rodent exclusion effects on each date using pairwise contrasts on estimated means (Lenth et al., 2018).

(4) *Do the impacts of seed predation on CWM track interannual differences in climate?* For each year, site, and season, we determined the magnitude of change in CWM by using the *RII* for CWM, calculated for the subset of the rodent-responsive community, which excluded creosotebush and grasses. We regressed this effect size against climate data for each site \times season combination using a linear model (function `gls` in `<nlme>`) fit with maximum likelihood (Pinheiro et al., 2017). We used model selection via the second-order *AICc* (Bartoń, 2013) to determine the best climate predictor from seasonal cumulative precipitation, annual cumulative precipitation, the *SPEI* drought index over a 6-month or 12-month integration period (Vicente-Serrano et al., 2010), or growing degree days (April–September) with a base air temperature of 0°C. Each climate variable was also included in models with a lag of one year to account for a possible delay in the plant response to rodent exclusion. The magnitude of rodent exclusion impacts on plant communities could vary temporally due to the differences in rates of seed predation or through indirect pathways, such as soil disturbances by rodent nests and burrows or altered competition between forbs and dominant grasses. Thus, we also explored how spatio-temporal variability in rodent-caused soil disturbances (data package: Lightfoot & Rudgers, 2021) or grass cover influenced the effect of rodent exclusion on CWM (Appendix S1: Figures S1 and S2).

RESULTS

(1) *Rodent exclusion altered plant community composition over a long time scale.* Rodent exclusion significantly altered the composition of monsoon plant communities in both grassland and shrubland sites (Table 1, Figure 2). In contrast, rodent exclusion had no significant influence on community composition during spring seasons (Appendix S1: Table S2). In the grassland, several common forb species increased from 1- to 20-fold in average cover under rodent exclusion, as revealed by SIMPER analysis (Appendix S1: Table S3). These included *Krascheninnikovia lanata* (Chenopodiaceae, 1890% increase in average cover under exclusion relative to control), *Chaetopappa ericoides* (Asteraceae, 990%), *Atriplex canescens* (Chenopodiaceae, 100%), and *Sphaeralcea leptophylla* (Malvaceae, 91%). In shrubland, common plant species that increased under rodent exclusion included *Opuntia phaeacantha* (Cactaceae, 1600% increase), *Senecio flaccidus* (Asteraceae, 1000% increase), and *Gutierrezia sarothrae* (Asteraceae, 90%) (Appendix S1: Table S3). When analyzing the whole plant community (Appendix S1: Table S1), several grasses in shrubland increased with rodent exclusion during the monsoon season, notably *Bouteloua eriopoda* (1400%), *Muhlenbergia porteri* (460% increase), *Sporobolus*

TABLE 1 Statistical results from analyses of monsoon season focal plant community structure excluding foundation plant species (grasses and creosotebush)

	Composition		Dispersion		Diversity		Richness	
	Pseudo- <i>F</i>	<i>p</i>	Pseudo- <i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Monsoon grassland								
Exclusion	19.06	0.0001	14.55	0.0005	0.81	0.4030	0.46	0.5222
Exclusion × year	0.51	0.9999	3.12	0.0202	1.14	0.3206	1.70	0.0535
Year	5.75	0.0001	8.86	0.0001	245.14	<0.0001	373.82	<0.0001
Monsoon shrubland								
Exclusion	5.34	0.0001	0.11	0.7774	0.57	0.4801	0.62	0.4597
Exclusion × year	1.16	0.1048	6.59	0.0001	55.61	<0.0001	92.67	<0.0001
Year	5.99	0.0001	7.35	0.0001	3.74	<0.0001	3.07	0.0001

Note: Results are presented for composition (PERMANOVA), beta-diversity (PERMDISP), diversity (Shannon H' index), and species richness for each habitat. $p < 0.05$ are in bold.

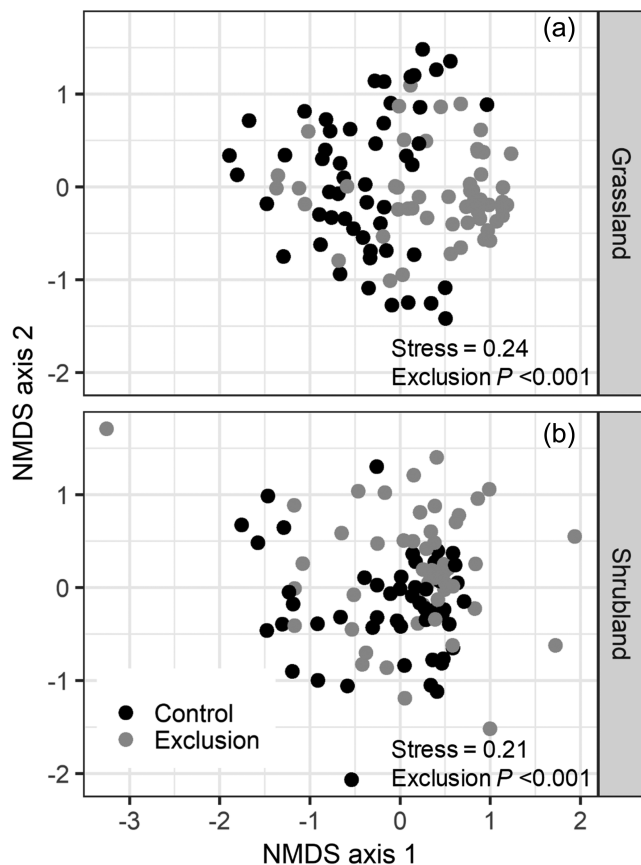


FIGURE 2 Non-metric multidimensional scaling (NMDS) plots of focal monsoon season plant species community composition in (a) grassland and (b) shrubland, excluding the dominant foundation species (grasses and creosote bush). Each point is a plot in a single year (1996–2008). Control plots, black symbols, rodent exclusion plots, gray symbols. Stress values from the ordinations are provided on each panel. Full statistical results are provided in Table 1

cryptandrus and *S. flexuosus* (>200%), *Aristida purpurea* (180%), *Dasyochloa pulchella* (150%), *Pleuraphis jamesii* (120%), and *Muhlenbergia arenicola* (50%). However, rodent exclusion did not significantly affect total grass cover across all grass species in either ecosystem type (Figure 3a,b, Grassland, Exclusion $p = 0.95$; Shrubland, Exclusion $p = 0.51$), and the only significant difference occurred in the grassland in 2007 (Figure 3a, $p = 0.035$).

(2) Rodent exclusion weakly influenced plant species diversity. Rodent exclusion had weak effects on plant alpha diversity and species richness (Table 1). Specifically, shrubland communities in spring shrubland and monsoon seasons had significant exclusion treatment × year interactions for either diversity or richness, but no pairwise contrasts between treatments within any year were statistically significant in either the full plant community (all $p > 0.06$, Appendix S1: Table S1, Figure S3) or the focal community that excluded grasses and creosotebush (Appendix S1: Table S2).

(3a) Large seed size predicted increase in plant biomass under rodent exclusion. Forb species with large seeds were significantly more likely to increase under rodent exclusion than species with small seeds (\ln [seed mass]; slope = 0.25 ± 0.087 SE, $F = 8.18$, $p = 0.008$, $R^2 = 0.22$, $N = 26$ species). As a result of the differences in plant species composition, this effect was slightly weaker in the more diverse grassland (Figure 4a; slope = 0.20 ± 0.099 SE, $F = 3.92$, $p = 0.063$, $R^2 = 0.18$, $N = 20$ species) than in shrubland (Figure 4b; slope = 0.51 ± 0.176 SE, $F = 8.61$, $p = 0.019$, $R^2 = 0.52$, $N = 10$). In the most conservative analysis, which used the average RII across all time points for all species with cover >0.1%, the relationship with seed size was neutral (Appendix S1: Figure S4; slope = -0.01 ± 0.009 SE, $F = 1.16$, $p = 0.293$, $R^2 = 0.05$,

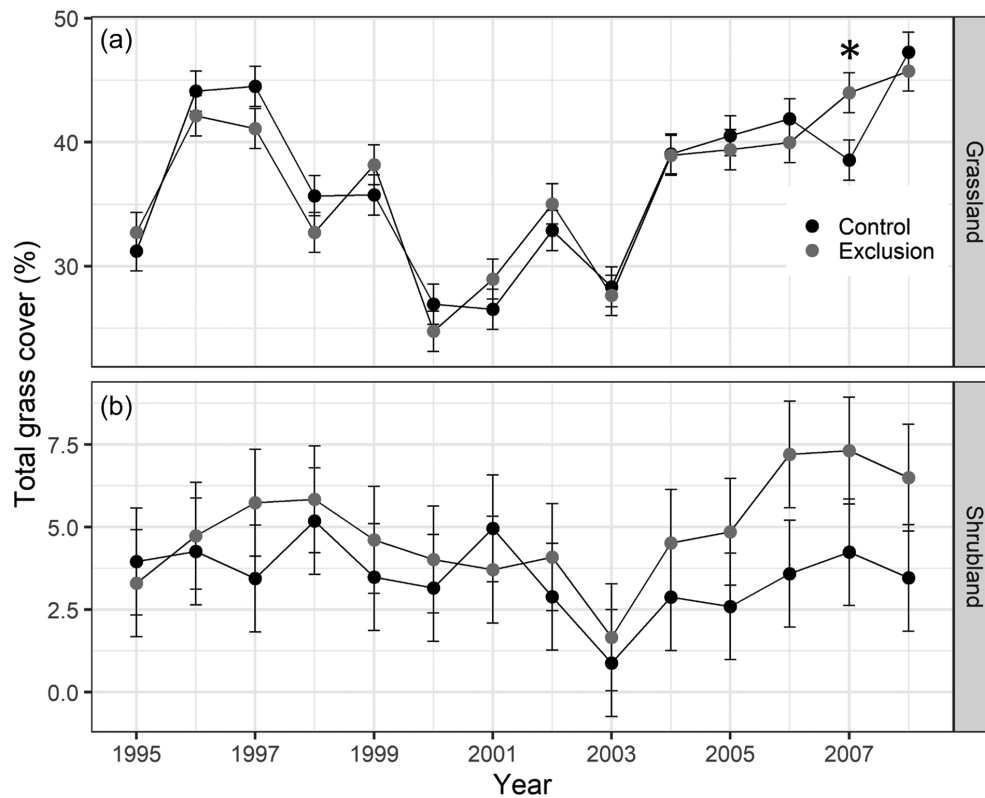


FIGURE 3 Total grass cover by rodent exclusion treatment over time showing means with SE for (a) grassland and (b) shrubland ecosystems. Exclusion $F = 0.42$, $p = 0.53$, exclusion \times ecosystem $F = 0.44$, $p = 0.52$. Although exclusion \times site \times year was statistically significant, $F = 4.74$, $p < 0.0001$, all exclusion effects were non-significant ($p > 0.05$) in all pairwise contrasts except in grassland in 2007

$N = 26$ species) because the cover of individual plant species was so dynamic over time.

(3b) *Rodent exclusion increased community-weighted seed mass.* Rodent exclusion increased CWM, most strongly in grassland focal communities (Figure 5, Table 2). Mean community seed mass was 1.27 g (median = 0.83) in monsoon grassland, 1.1 g in spring grassland, and less than half of that (only 0.5 g [median = 0.18 g]) in shrubland during both seasons. The range was similar, with a maximum of 5.6 g seed mass at both sites, and within a site, CWM did not significantly differ between seasons. In the whole community analysis, which included grasses and creosotebush, rodent exclusion did not increase CWM, although there was a significant rodent exclusion \times year \times ecosystem type interaction (Figure S5).

In the grassland, CWM increased during the monsoon season, on average by 60% inside versus outside of rodent exclosures. The largest effect sizes occurred in 1999 (130% increase), 2003 (230% increase), and 2007 (140% increase), (Figure 5a). During spring season, rodent exclusion did not significantly alter grassland CWM in any year (Figure S6). Skewness of the grassland seed size distribution was affected only in 2004, with an expected decline in skewness by 55% under rodent

exclusion (ecosystem \times exclusion \times year, $p < 0.0001$; 2004 grassland: $p = 0.031$). Rodent exclusion had no significant influence on kurtosis of the grassland seed size distribution in any year ($p > 0.14$). As predicted under the expectation that rodents select seeds based on size, variance in seed size increased under rodent exclusion in both the ecosystems only during fall ($p = 0.0025$), not in spring ($p = 0.69$). In grassland, variance in seed size distribution during fall was 83% greater under rodent exclusion than in control plots.

In shrubland, rodent exclusion increased CWM during the monsoon season by just 8% on average over all the years, but the effects were more temporally variable than in grassland. Rodent exclusion increased shrubland CWM by a maximum of 1190% in monsoon in 2003, with a 160% increase in 2004, and 70% in 2001 (Figure 5b). Other aspects of the distribution of community seed size were affected in some years in shrubland. In shrubland plant community during the monsoon season, variance in community seed size increased under rodent exclusion by 66% as in the grassland. In contrast to the grassland, the spring season shrubland CWM increased under rodent exclusion in 2003 and 2007 (Appendix S1: Figure S6). As predicted, skewness declined by 123% with rodent exclusion in 2007 ($p < 0.0001$); but kurtosis increased, in

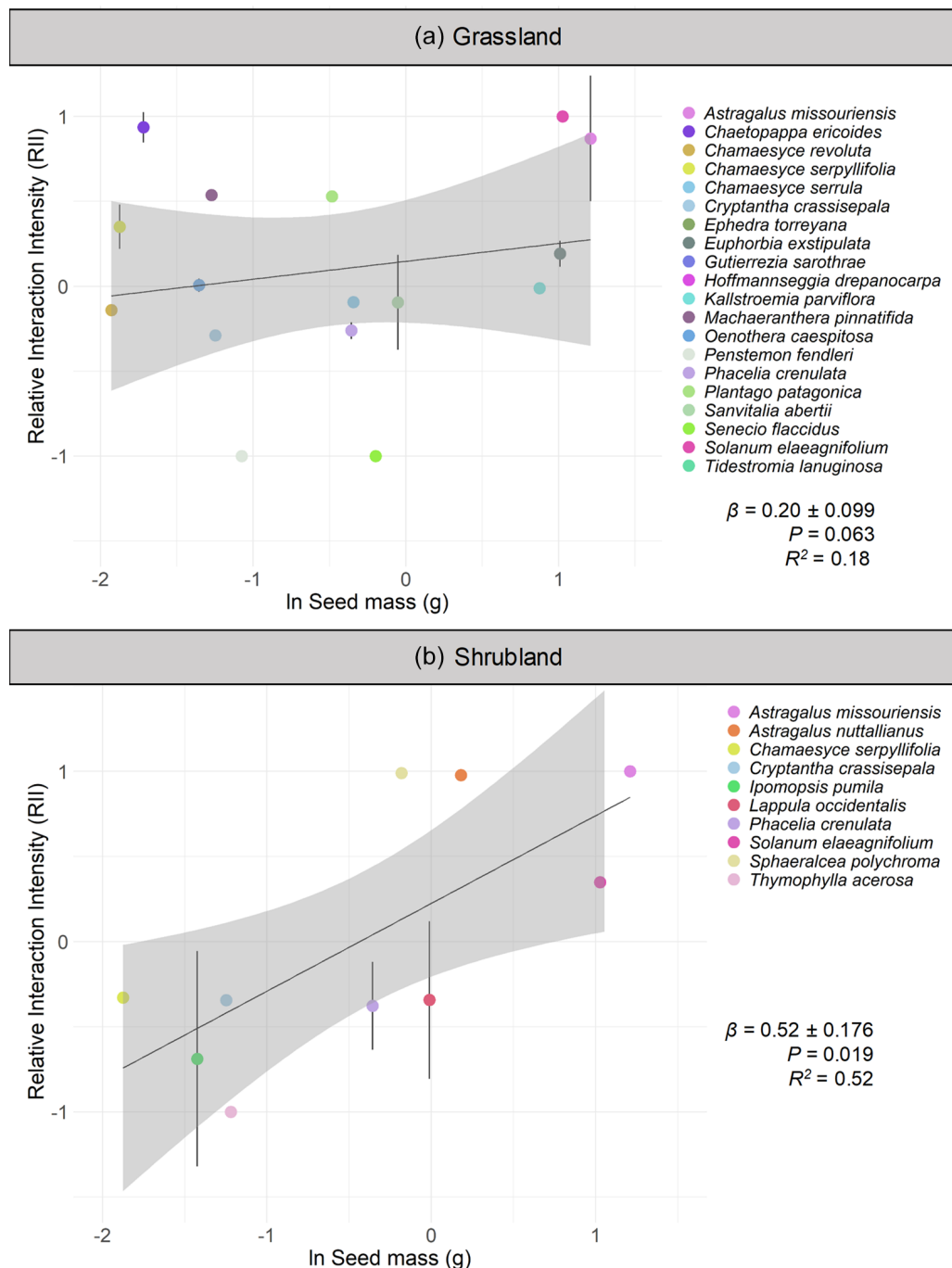


FIGURE 4 Plant species with larger seed mass had greater increases in percentage cover inside versus outside of rodent exclosures in the (a) grassland, $N = 20$ plant species and (b) shrubland, $N = 10$ species. RII is the relative interaction intensity, a measure of species' effect sizes for their responsiveness to rodent exclusion that scales from -1 to 1 . Bars show standard deviation following Armas et al. (2004). Seed mass is plotted on a \ln scale

contrast to our prediction that the presence of rodent would create a more peaked seed size distribution. Kurtosis was 455% greater under rodent exclusion in 1999 ($p < 0.0001$), 218% in 2004 ($p < 0.0001$), and 60% in 2005 ($p < 0.0001$; ecosystem \times exclusion \times year, $p < 0.0066$).

(4) *Rodent effects on community-level seed mass were strongest during dry periods.* The magnitude of increase in

CWM under rodent exclusion was greatest during the driest periods in both grassland and shrubland (Figure 6). Monsoon CWM in the grassland had the strongest relationship with seasonal precipitation (Figure 6a), barely outranking annual precipitation by $\Delta AICc$ 2.1, and outranking all other climate variables by $\Delta AICc > 3.4$. For the monsoon shrubland, the drought index for

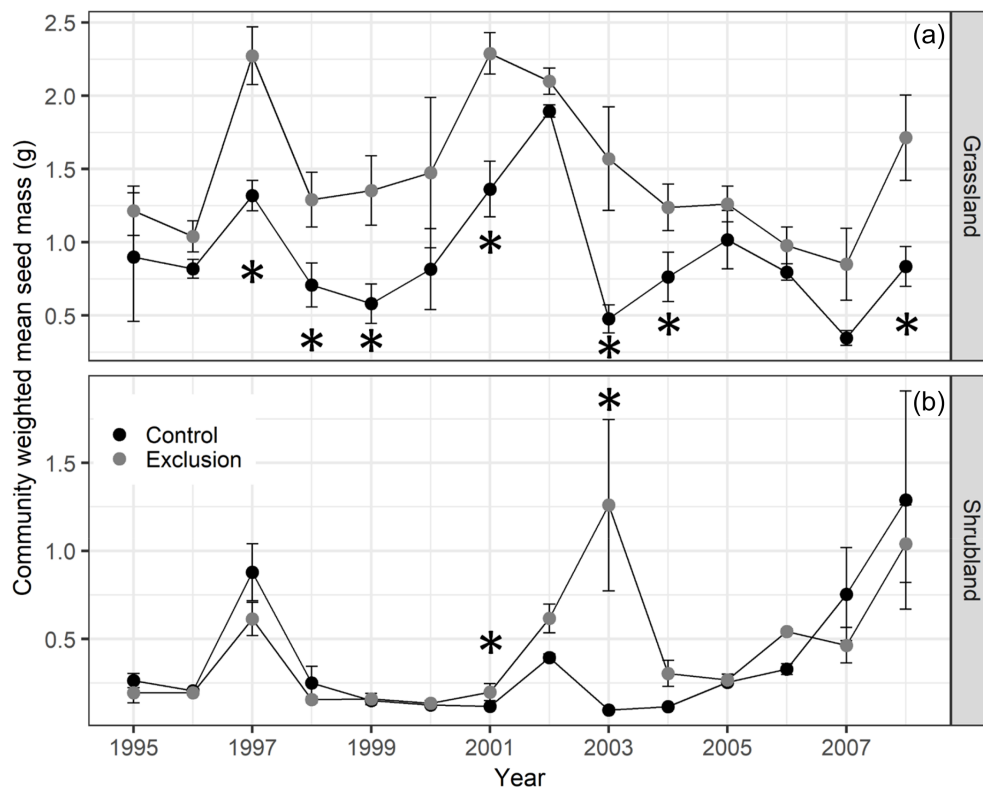


FIGURE 5 Community seed mass (CWM) in control (black symbols) and rodent exclusion (gray symbols) plots for (a) grassland and (b) shrubland monsoon plant communities. Community-weighted seed mass excludes grasses and creosotebush. Symbols show the treatment mean \pm SE calculated after averaging quadrats within plots. Asterisks indicate years with significant rodent exclusion effects

TABLE 2 Results from general linear mixed-effects models for community seed mass (g) \sim exclusion treatment \times year for each ecosystem type

Effect	F	p
Monsoon grassland		
Exclusion treatment	11.05	0.0159
Exclusion \times year	3.09	0.0001
Year	17.14	<0.0001
Monsoon shrubland		
Exclusion treatment	0.19	0.6759
Exclusion \times year	4.92	<0.0001
Year	2.55	0.0028

Note: The full model included the repeated, random effects of plot identity (nested in exclusion treatment and ecosystem) and quadrat (nested within plot) as well as AR2 temporal autocorrelation. Grassland model marginal $R^2 = 0.12$, conditional $R^2 = 0.38$. Shrubland model marginal $R^2 = 0.19$, conditional $R^2 = 0.24$. p -values <0.05 are shown in bold.

April–September of the previous year was the best climate predictor (Figure 6b), and the next best model was lagged seasonal precipitation, suggesting a delayed response of rodent impacts on shrubland communities. Spring plant

communities had weaker and opposite sensitivities to climate than monsoon season communities. Here, the magnitude of increase in CWM under rodent exclusion was greatest during wetter years in the grassland or hotter years in shrubland (Figure 7), but climate influences for spring community responses were non-significant.

DISCUSSION

Large-seeded species increased in abundance under rodent exclusion, but responses were mediated by climate

Our results demonstrate that the long-term impacts of granivorous rodents on plant communities can be substantial, but the magnitude of these effects varied among ecosystem types, seasons, and years. Rodents strongly influenced the community composition and seed size distribution in two northern Chihuahuan Desert plant communities, with these effects tied to variation in precipitation and drought. Such climatic variability is a hallmark of drylands and has been escalating under climate change (Maurer et al., 2020). In both grassland and shrubland vegetation, the strongest

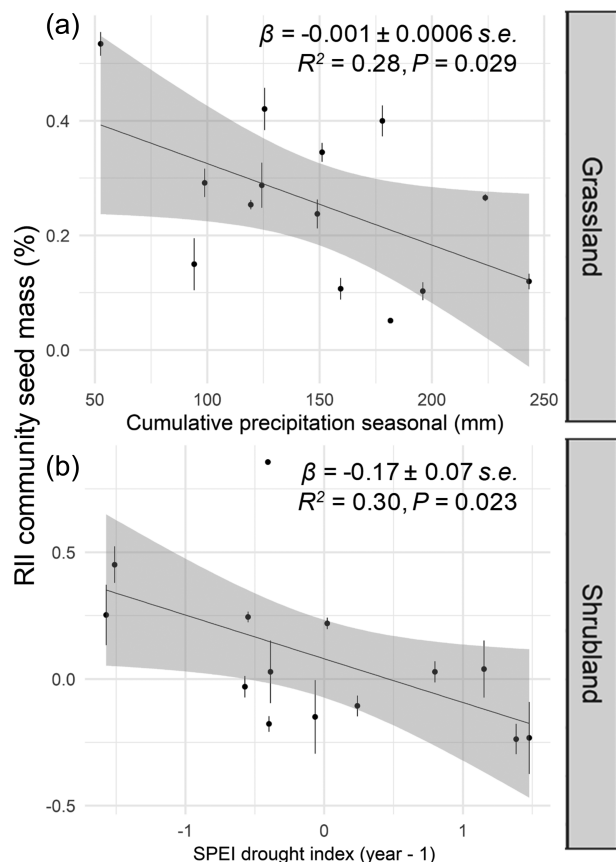


FIGURE 6 Magnitude of increase in community seed mass (CWM) for monsoon season focal plant assemblages (excluding grasses and creosotebush) in (a) grassland and (b) shrubland. The effect size (*RII*) was determined from yearly means as $(\text{Mean}_{\text{Exclusion}} - \text{Mean}_{\text{Control}})/(\text{Mean}_{\text{Control}} + \text{Mean}_{\text{Control}})$ with the SD following Armas et al. (2004). *RII* is plotted as a function of the best climate predictor. Large values of SPEI indicate wetter/cooler years. The slope (β), R^2 , and p -value from a hypothesis test that $\beta = 0$ are provided for each ecosystem type

general pattern was a substantial increase in the abundance of larger-seeded forb species in response to rodent exclusion. This was manifested at the community level as larger CWM and greater variance in seed mass of the forb communities inside versus outside of rodent exclosures.

In many open habitats, where seed sizes are smaller than in forests, large-seeded species are highly vulnerable to seed predation (Abramsky, 1983; Maron et al., 2012, 2018; Reader, 1993). A recent world-wide review and meta-analysis (Dylewski et al., 2020) revealed that in open habitats, such as grasslands, large seeds were the most sensitive to small mammal predation. Our results mirror those of Brown and Heske (1990) who similarly observed large-seeded species increase inside rodent exclosures after many years of rodent exclusion. However, the long-term experiment by Brown and colleagues additionally filtered rodent communities by rodent size

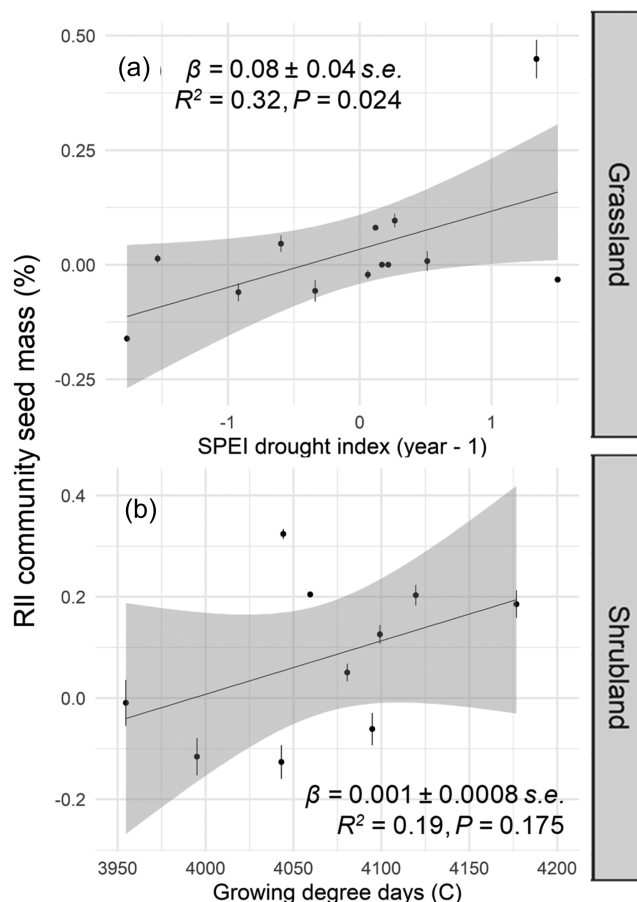


FIGURE 7 Magnitude of increase in community seed mass (CWM) as a function of the best climate predictor for (a) grassland and (b) shrubland ecosystem, for the spring season focal plant community excluding grasses and creosotebush. Large values of SPEI indicate wetter/cooler years. Y-axis values were determined from yearly means and SE as $\text{RII} = (\text{Mean}_{\text{Exclusion}} - \text{Mean}_{\text{Control}})/(\text{Mean}_{\text{Control}} + \text{Mean}_{\text{Control}})$ and are shown with the SD for *RII* following Armas et al. (2004). The slope (β), R^2 , and p -value from a hypothesis test that $\beta = 0$ are provided for each ecosystem

and detected the strongest influences when the largest rodents (kangaroo rats) were excluded. Novel to our study was that plant community responses to rodent exclusion varied spatially between grassland and shrubland and temporally between spring and monsoon seasons. These results are important because they indicate how ecosystem state transitions and climate change could reshape communities through altered species interactions (e.g., Urban et al., 2017).

Rodent impacts on plant community diversity

Contrary to our original hypothesis, rodent exclusion did not strongly influence plant species diversity or richness

(see Báez et al., 2006). Although rodent seed predation decreased the abundance of particular large-seeded species, predation was not strong enough to eliminate these species from the community or to reorder species abundances so drastically as to alter overall species diversity. Our findings contrast with results from other long-term consumer exclusions in which insects or ungulates increase alpha diversity by suppressing plant community dominants (Carson & Root, 2000; Koerner et al., 2018; Olff & Ritchie, 1998). However, a long-lived seed bank in our system may buffer species against local extirpation. Seeds in a seedbank are generally less vulnerable to predation than newly dispersed seeds on soil surfaces (Clark et al. 2007; Hulme, 1994).

Context-dependency of top-down impacts of rodents: Ecosystem type

A consistent feature of plant–consumer interactions is that they are highly context-dependent; interaction strength varies across space and/or over time (Chamberlain et al., 2014; Maron et al., 2014; Werner et al., 2020). In the northern Chihuahuan Desert, the grassland and shrubland ecosystems we studied differed in the identity of the dominant plant species, the amount of open space for seed germination (less in grassland than shrubland; Pockman & Small, 2010), plant diversity (higher in grasslands than shrublands; Appendix S1: Figures S3 and S7), the density and size of rodents (50% fewer animals in grasslands than shrublands; Báez et al., 2006; Cárdenas et al., 2021), the amount of rodent-caused soil disturbance (54% greater in grasslands [mean = 37%] than shrublands [mean = 24%]; Appendix S1: Figure S1), and caching behavior of rodents (Jenkins & Breck, 1998; Yeakel et al., 2020). Not surprisingly, plant community responses to rodent exclusion differed between these ecosystem types, likely as a consequence of these differences. The increase in CWM seed mass with rodent exclusion was 52% larger, on average, in grassland than shrubland (Figure 5), and the increase in variance of the seed mass distribution was also greater in the grassland than shrubland. These results are perhaps not surprising, given the greater plant diversity in grassland than shrubland, combined with the greater number of species with larger seed sizes that are likely more vulnerable to seed predation. Decomposing the factors underlying ecosystem-context dependency may require rodent exclusions imposed together with manipulations of hypothesized mechanisms, such as soil disturbance, plant diversity, or the amount of bare ground.

In contrast to the larger response in CWM seed mass to rodent exclusion in grassland, the relationship between individual plant species responses to rodent

exclusion and their seed size was stronger in shrubland (Figure 4). Notably, this was not driven by responses of *large-seeded* species to rodent exclusion, as occurred in grassland. Instead, in shrubland, small-seeded species *declined* under rodent exclusion (Figure 4). One explanation is that shrublands had greater dominance of *Dipodomys* species than grasslands (Cárdenas et al., 2021), and extensive soil disturbances caused by these large rodents in shrublands facilitated the recruitment of small-seeded species outside of exclosures. On average, soil disturbance attributed to rodents was much lower in shrubland than grassland, although rodent exclusion significantly reduced disturbance on more dates in shrubland than grassland (in spring; Appendix S1: Figure S1). Other studies have shown that large effects of *Dipodomys* on plant communities can be caused by their ecosystem engineering (e.g., Prugh & Brashares, 2012) and may interact with additional disturbances, such as fire (e.g., Nicolai, 2019).

Context-dependency of top-down impacts of rodents: Climate variability

Substantial interannual variation in the impacts of rodent exclusion on plant communities tracked interannual differences in climate, as we originally hypothesized. It has become drier and more variable over the past 100 years at our sites (Rudgers et al., 2018) and regionally (Maurer et al., 2020). In monsoon plant communities, where the response to rodent exclusion was the greatest, rainfall, either during the current year (grassland) or previous year (shrubland), correlated negatively with increases in CWM caused by rodent exclusion. In dry periods, large-seeded species responded more positively to rodent exclusion than during wetter periods in both ecosystems. However, we suspect that different mechanisms operate in grassland versus shrubland to influence the context-dependency of rodent impacts. In grasslands, climate influences occurred in concurrent arid periods, whereas in shrubland, the impacts of rodent exclusion were greatest when lagged by one year. We speculate that in shrubland, drought altered both the foraging decisions and abundances of rodents during arid years, causing lagged effects manifest through the seed bank in the subsequent year. A stochastic dynamic program that modeled rodent foraging decisions predicted altered food preferences under resource limitation, particularly for rodents weighing less than 50 g (Yeakel et al., 2020). In grassland, we hypothesize that dry conditions instead influenced the process of plant recruitment by reducing total plant cover and opening safe sites for seedlings in the more densely vegetated grassland.

Isolating the underlying causes of climate-context dependency in rodent exclusion is complex. Desert rodent communities are dynamic and change in nonlinear ways with variable resources (Brown & Ernest, 2002; Guo & Brown, 1996; Lima et al., 2008; Thibault et al., 2010). In our system, as in others, rodent abundances are often best predicted by the previous year's precipitation or aridity (Báez et al., 2006; Cárdenas et al., 2021; Thibault et al., 2010), likely because increased primary production boosts rodent reproduction, rather than reducing survival, creating a time lag in the response of population abundance (e.g., Lightfoot et al., 2012). Linking rodent abundance with when rodents have the largest effects on plant communities is not straightforward because of the divergent responses in abundance as well as foraging behaviors among rodent species. For example, in a recent regional analysis of rodent abundance and climate, *D. spectabilis* increased during wet years in both the grassland and shrubland sites studied here. *D. merriami* (only abundant in shrubland) increased the year following a wet year, and *D. ordii* (only abundant in grassland) was largely insensitive to aridity (Cárdenas et al., 2021). However, the abundance of another heteromyid that has large abundance spikes, the silky pocket mouse (*Perognathus flavus*), which nonlinearly tracked drought, was most abundant in or following wet or dry extremes in both grassland and shrubland (Noble et al., 2019; Cárdenas et al., 2021). Moreover, other factors, such as the relative abundance of preferred plant species, competition with other consumers (Brown et al., 2001; Brown et al., 2002; Brown & Heske, 1990; Lima et al., 2008), predation and risk of predation (Kotler, 1984; Lima et al., 2002; Meserve et al., 2003; Stapp & Polis, 2003), influence rodent foraging pressure. Finally, years that are best for plant recruitment, when past effects of granivory can be manifested, are not always times when rodent abundance is highest. Therefore, disentangling the extent to which our results were influenced by the direct effects of climate on rodent abundance and/or foraging behavior as opposed to the effects of climate on plant recruitment is not possible without additional experimentation, such as climate manipulations (e.g., drought shelters, water additions, etc.) crossed with rodent exclusion.

Context-dependency of top-down impacts of rodents: Seasonal variability

The magnitude of plant community responses to rodent exclusion varied seasonally. In general, the community that establishes with monsoon rains had a greater response to rodent exclusion than did the assemblage that recruits

during spring. The probable reason for the greater monsoon responses to rodent exclusion is that plant biomass of non-foundation plant species was generally larger during the summer monsoon than in spring, as was plant species richness (i.e., fall plant community; Appendix S1: Figure S3). Thus, there was simply more scope for detecting a response in the monsoon season than in spring. Moreover, some rodents switch from eating insects in spring to focusing on more abundant seeds during the late summer monsoons (Noble, 2017; Schooley et al., 2018), which could also contribute to the larger response of the monsoon versus spring plant assemblage. It is unlikely that seasonal differences in the effects of rodent exclusion were due to seasonal differences in rodent-caused disturbance to soils, as this was greatest in spring (Appendix S1: Figure S1). The greater impact of rodent exclusion during the monsoon season was also not generally due to larger-seeded species occurring more frequently in monsoon than spring because CWM did not differ seasonally.

Rodent-mediated disturbances

In a previous long-term rodent exclusion study in the western Chihuahuan Desert, Brown and Heske (1990) similarly found that long-term rodent exclusion had strong effects on the plant community. In this and other studies, rodents can influence plant communities not only through the direct effects of predation on larger-seeded plant species, but also through indirect effects of reduced soil disturbance that result from rodent exclusion (Brown & Heske, 1990; Prugh & Brashares, 2012). In our study, some lines of evidence support the hypothesis that in grassland the impacts of rodent exclusion on seed mass occurred in-part through the indirect effect of rodents on soil disturbance, and via competition with grass. First, grass cover in grassland was, on average, more than 9-fold greater than in shrubland (Grassland mean = 37%, Shrubland mean = 4%; Figure 3), and soil disturbance was on average 50% greater (Appendix S1: Figure S1). Thus, it is likely that any indirect effects of rodent disturbance would be strongest in grasslands. Second, rodent disturbance to soils was greatest in dry years (Appendix S1: Figure S1) when grass cover also significantly declined. Although losses in grass cover occurred in both rodent exclusion and control plots during dry years (Figure 3), a general reduction in grass cover may enable differences in the seedbank that are caused by seed predation to manifest by opening more space for seedling recruitment. Finally, CWM declined with grass cover in both treatments in grassland (Appendix S1: Figure S2). Altogether, these correlations suggest that the indirect effects of reduced grass cover

and increased soil disturbance may partially explain why community seed size increased the most in dry years in grassland. Clearly, a full exploration of both the direct and indirect pathways through which rodents influence the plant community requires a formal path analyses via structural equation modeling. Our study lacked the replication at each time point that is needed for sufficient statistical power to disentangle direct and indirect pathways of climate and rodents on the plant community.

In contrast to the grassland, our results in shrubland did not appear influenced by rodent disturbance or changes in grass cover. The correlation between grass cover and the CWM of non-grasses was half as strong in exclusion plots as in controls (Appendix S1: Figure S2). Generally, grasses in shrubland did not respond to yearly differences in aridity (marginal $R^2 = 0.006$) or rainfall (marginal $R^2 = 0.007$). Together, these results are consistent with the hypothesis that there was no release from competition with grasses in dry years in the shrubland ecosystem. Possibly, rodents consumed more grass cover during wet years because nutritious resources were more limited in shrubland (e.g., Kerley et al., 1997; Yeakel et al., 2020). Average plant cover excluding grasses and creosotebush was just 1.8% in the monsoon shrubland versus 6.5% in grassland. In shrubland, a 2-fold stronger negative correlation between CWM and grass cover occurred in the presence versus absence of rodents (Appendix S1: Figure S2), which could indicate that rodents spent more time eating non-grass plants in patches with high grass cover in order to shelter from predators in the sparsely vegetated shrubland. More rigorous evaluation of the relative contribution of soil disturbance versus direct seed predation in affecting the plant community will require experimental manipulation of soil disturbance and/or seed predation in ways that would mimic rodent effects.

CONCLUSION

Altogether, 15 years of rodent exclusion experiments in northern Chihuahuan Desert grassland and shrubland revealed important, but climate-sensitive, shifts in plant traits. Seed size at the community level increased under rodent exclusion, driven by the recruitment responses of several large-seeded forb and shrub species in grassland, which increased in the absence of rodents, and several small-seeded species in shrubland, which decreased in the absence of rodents. The strength of the influence of rodent exclusion on the plant community, particularly on community seed size, was greatest in dry years, or in years following dry years and for plants that dominated during the monsoon season. As drylands in southwestern North

America become increasingly drier in the future, our results suggest the impacts of rodents on plant communities, and plant community-level traits, may intensify.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT


All data and code (Lightfoot & Rudgers, 2021) are available from the Environmental Data Initiative: <https://doi.org/10.6073/pasta/84841a70dd8cc89b9a5716e3511cc3a4>.

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REFERENCES

- Abramsky, Z. 1983. "Experiments on Seed Predation by Rodents and Ants in the Israeli Desert." *Oecologia* 57: 328–32.
- Abramsky, Z. 1988. "The Role of Habitat and Productivity in Structuring Desert Rodent Communities." *Oikos* 52: 107–14.
- Albert, M.J., A. Escudero, and J.M. Irionodo. 2005. "Assessing Ant Seed Predation in Threatened Plants: A Case Study." *Acta Oecologica* 28: 213–20.
- Angert, A.L., T.E. Huxman, P. Chesson, and D. Lawrence Venable. 2009. "Functional Tradeoffs Determine Species Coexistence Via the Storage Effect." *Proceedings of the National Academy of Sciences of the United States of America* 106: 11641–5.
- Armas, C., R. Ordiales, and F.I. Pugnaire. 2004. "Measuring Plant Interactions: A New Comparative Index." *Ecology* 85: 2682–6.
- Báez, S., S.L. Collins, D. Lightfoot, and T.L. Koontz. 2006. "Bottom-Up Regulation of Plant Community Structure in an Arid Ecosystem." *Ecology* 87: 2746–54.
- Bartoń, K. 2013. "Model Selection and Model Averaging Based on Information Criteria (AICc and Alike). MuMIn: Multi-Model Inference." R package version 1.15.6. R Foundation for Statistical Computing, Vienna, Austria. <http://cran.r-project.org/web/packages/MuMIn/index.html>.

- Bricker, M., D.E. Pearson, and J.L. Maron. 2010. "Small Mammal Seed Predation Limits the Recruitment and Abundance of Two Perennial Grassland Forbs." *Ecology* 91: 85–92.
- Brown, J.H., and M.S.K. Ernest. 2002. "Rain and Rodents: Complex Dynamics of Desert Consumers." *BioScience* 52: 979–87.
- Brown, J.H., and E.J. Heske. 1990. "Control of a Desert–Grassland Transition by a Keystone Rodent Guild." *Science* 250: 1705–7.
- Brown, J.H., T.G. Whitham, and S.K.M. Ernest. 2001. "Complex Species Interactions and the Dynamics of Ecological Systems: Long-Term Experiments." *Science* 293: 643–50.
- Brown, J.H., D.A. Kelt, and B.J. Fox. 2002. "Assembly Rules and Competition in Desert Rodents." *American Naturalist* 160: 815–8.
- Cárdenas, P.A., E.M. Christensen, S.K.M. Ernest, D.C. Lightfoot, R. L. Schooley, P. Stapp, and J.A. Rudge. 2021. "Declines in Rodent Abundance and Diversity Track Regional Climate in North American Drylands." *Global Change Biology* 27: 4005–23. <https://doi.org/10.1111/gcb.15672>
- Carson, W.P., and R.B. Root. 2000. "Herbivory and Plant Species Coexistence: Community Regulation by an Outbreking Phytophagous Insect." *Ecological Monographs* 70: 73–99.
- Chamberlain, S.A., J.L. Bronstein, and J.A. Rudgers. 2014. "How Context-Dependent Are Species Interactions?" *Ecology Letters* 17: 881–90.
- Clark, C.J., J.R. Paulsen, D.J. Levey, and C.W. Osenberg. 2007. "Are Plant Populations Seed Limited? A Critique and Meta-analysis of Seed Addition Experiments." *American Naturalist* 170: 128–42.
- Clarke, K.R., and R.N. Gorley. 2009. *Primer Version 6.1.10 User Manual and Tutorial*. Plymouth: Primer-E.
- Collins, S.L., Y. Anny Chung, L.E. Baur, A. Hallmark, T.J. Ohlert, and R.A. Rudgers. 2020. "Press-Pulse Interactions and Long-Term Community Dynamics in a Chihuahuan Desert Grassland." *Journal of Vegetation Science* 31: 722–32.
- Connolly, B.M., D.E. Pearson, and R.N. Mack. 2014. "Granivory of Invasive, Naturalized, and Native Plants in Communities Differentially Susceptible to Invasion." *Ecology* 95: 1759–69.
- Crawley, M.J. 1992. "Seed Predators and Plant Population Dynamics." In *Seeds: The Ecology of Regeneration in Plant Communities*, edited by M. Fenner, 157–92. Wallingford, CT: CAB International.
- Curtin, C.G., D.A. Kelt, T.C. Frey, and J.H. Brown. 1999. "On the Role of Small Mammals in Mediating Climatically Driven Vegetation Change." *Ecology Letters* 2: 309–17.
- Davidson, D.W., D.A. Samson, and R.S. Inouye. 1985. "Granivory in the Chihuahuan Desert: Interactions within and between Trophic Levels." *Ecology* 66: 486–502.
- Davidson, A.D., E. Ponce, D.C. Lightfoot, E.L. Fredrickson, J.H. Brown, J. Cruzado, S.L. Brantley, et al. 2010. "Rapid Response of a Grassland Ecosystem to an Experimental Manipulation of a Keystone Rodent and Domestic Livestock." *Ecology* 91: 3189–200.
- Dick-Peddie, W.A. 1993. *New Mexico Vegetation*. Albuquerque, NM: University of New Mexico Press.
- Dylewski, L., Y.K. Ortega, M. Bogdziewicz, and D.E. Pearson. 2020. "Seed Size Predicts Global Effects of Small Mammal Seed Predation on Plant Recruitment." *Ecology Letters* 23: 1024–33.
- Ernest, S.K.M., J.H. Brown, and R.R. Parmenter. 2000. "Rodents, Plants, and Precipitation: Spatial and Temporal Dynamics of Consumers and Resources." *Oikos* 88: 470–82.
- Ferreira, A.V., E.M. Bruna, and H.L. Vasconcelos. 2011. "Seed Predators Limit Plant Recruitment in Neotropical Savannas." *Oikos* 120: 1013–22.
- Funk, J.L., J.E. Larson, G.M. Ames, B.J. Butterfield, J. Cavender-Bares, J. Firn, D.C. Laughin, A.E. Sutter-Grier, L. Williams, and J. Wright. 2017. "Revisiting the Holy Grail: Using Plant Functional Traits to Understand Ecological Processes." *Biological Reviews* 92: 1156–73.
- Gaedke, U., and T. Klauschies. 2017. "Analyzing the Shape of Observed Trait Distributions Enables a Data-Based Moment Closure of Aggregate Models." *Limnology and Oceanography: Methods* 15: 979–94.
- Gherardi, L.A., and O.E. Sala. 2015. "Enhanced Precipitation Variability Decreases Grass- and Increases Shrub- Productivity." *Proceedings of the National Academy of Sciences of the United States of America* 112: 12735–40.
- Gross, N., Y.L. Bagousse-Pinguet, P. Liancourt, M. Berdugo, N.J. Gotelli, and F.T. Maestre. 2017. "Functional Trait Diversity Maximizes Ecosystem Multifunctionality." *Nature Ecology & Evolution* 1: 0132.
- Guo, Q.F., D.B. Thompson, T.J. Valone, and J.H. Brown. 1995. "The Effects of Vertebrate Granivores and Folivores on Plant Community Structure in the Chihuahuan Desert." *Oikos* 73: 251–9.
- Guo, Q., and J.H. Brown. 1996. "Temporal Fluctuations and Experimental Effects in Desert Plant Communities." *Oecologia* 107: 568–77.
- Gutiérrez, J.R., P.L. Meserve, S. Herrera, L.C. Contreras, and F.M. Jaksic. 1999. "Effects of Small Mammals and Vertebrate Predators on Vegetation in the Chilean Semiarid Zone." *Oecologia* 109: 398–406.
- Hernández, A.G., J.W. Romero, D. Lightfoot, E. Aragón, and J. López Portillo. 2005. "Changes in Rodent Community Structure in the Chihuahuan Desert Mexico: Comparisons Between two Habitats." *Journal of Arid Environments* 60: 239–57.
- Heske, E.J., J.H. Brown, and Q. Guo. 1993. "Effects of Kangaroo Rat Exclusion on Vegetation Structure and Plant Species Diversity in the Chihuahuan Desert." *Oecologia* 95: 520–4.
- Hope, A.G., and R.R. Parmenter. 2007. *Food Habits of Rodents Inhabiting Arid and Semi-Arid Ecosystems of Central New Mexico*. Museum of Southwestern Biology, Special Publication, Vol 9 1–75. Albuquerque, NM: Museum of Southwestern Biology.
- Hughes, J., D. Ward, and M. Perrin. 1994. "Predation Risk and Competition Affect Habitat Selection and Activity of Namib Desert Gerbils." *Ecology* 75: 1397–405.
- Hulme, P.E. 1994. "Postdispersal Seed Predation in Grasslands - Its Magnitude and Sources of Variation." *Journal of Ecology* 82: 645–52.
- Hulme, P.E. 2002. "Seed Eaters: Seed Dispersal, Destruction and Demography." In *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*, edited by D.J. Levey, M.G. Silva and M. Galetti, 257–73. Wallingford, UK: CAB International.
- Inouye, R.S., G. Byers, and J.H. Brown. 1980. "Effects of Predation and Competition on Survivorship, Fecundity and Community Structure of Desert Annuals." *Ecology* 61: 1344–51.
- Jenkins, S.H., and S.W. Breck. 1998. "Differences in Food Hoarding among Six Species of Heteromyid Rodents." *Journal of Mammalogy* 79: 1221–33.
- Kelt, D.A. 2011. "Comparative Ecology of Desert Small Mammals: A Selective Review of the Past 30 Years." *Journal of Mammalogy* 92: 1158–78.

- Kerley, G.I.H., W.G. Whitford, and F.R. Kay. 1997. "Mechanisms for the Keystone Status of Kangaroo Rats: Granivory Rather than Granivory?" *Oecologia* 111: 422–8.
- Koerner, S.E., M.D. Smith, D.E. Burkepile, N. Hanan, M.L. Avolio, S.L. Collins, A.K. Knapp, et al. 2018. "Change in Dominance Determines Herbivore Effects on Plant Biodiversity." *Nature Ecology & Evolution* 2: 1925–32.
- Kotler, B.P. 1984. "Risk of Predation and the Structure of Desert Rodent Communities." *Ecology* 65: 689–701.
- Kotler, B.P., and J.S. Brown. 1988. "Environmental Heterogeneity and the Coexistence of Desert Rodents." *Annual Review of Ecology and Systematics* 19: 281–307.
- Larios, L., D.E. Pearson, and J.L. Maron. 2017. "Incorporating the Effects of Generalist Seed Predators into Plant Community Theory." *Functional Ecology* 31: 1856–67.
- Lavorel, S., J. Storkey, R.D. Bardgett, F. De Bello, M.P. Berg, X. Le Roux, Marco Moretti, et al. 2013. "A Novel Framework for Linking Functional Diversity of Plants with Other Trophic Levels for the Quantification of Ecosystem Services." *Journal of Vegetation Science* 24: 942–8.
- Lefcheck, J.S. 2016. "PIECEWISESEM: Piecewise Structural Equation Modelling in R for Ecology, Evolution, and Systematics." *Methods in Ecology and Evolution* 7: 573–9.
- Lenth, R., H. Singmann, J. Love, P. Buerkner & M. Herve 2018. "Package 'emmeans': Estimated Marginal Means, Aka Least-Square Means. v1.3.0".
- Lightfoot, D., and J.A. Rudgers. 2021. *Small Mammal Exclosure Study (SMES) Vegetation Data from the Chihuahuan Desert Grassland and Shrubland at the Sevilleta National Wildlife Refuge, New Mexico (1995-2009)*. Environmental Data Initiative. <https://doi.org/10.6073/pasta/84841a70dd8cc89b9a5716e3511cc3a4>
- Lightfoot, D.C., A.D. Davidson, D.G. Parker, L. Hernández, and J.W. Laundré. 2012. "Bottom-Up Regulation of Desert Grassland and Shrubland Rodent Communities: Implications of Species-Specific Reproductive Potentials." *Journal of Mammalogy* 93: 1017–28.
- Lima, M., N.C. Stenseth, and F.M. Jaksic. 2002. "Population Dynamics of a South American Rodent: Seasonal Structure Interacting with Climate, Density Dependence and Predator Effects." *Proceedings of the Royal Society B* 269: 2579–86.
- Lima, M., S.K.M. Ernest, J.H. Brown, A. Belgrano, and N.C. Stenseth. 2008. "Chihuahuan Desert Kangaroo Rats: Nonlinear Effects of Population Dynamics, Competition, and Rainfall." *Ecology* 89: 2594–603.
- Longland, W.S. 2007. "Desert Rodents Reduce Seedling Recruitment of *Salsola Paulsenii*." *Western North American Naturalist* 67: 378–83.
- Longland, W.S., S.H. Jenkins, S.B. Vander Wall, J.A. Veech, and S. Pyare. 2001. "Seedling Recruitment in *Oryzopsis Hymenoides*: Are Desert Granivores Mutualists or Predators?" *Ecology* 82: 3131–48.
- Lucero, J.E., and R.M. Callaway. 2018. "Native Granivores Reduce the Establishment of Native Grasses but Not Invasive *Bromus Tectorum*." *Biological Invasions* 20: 3491–7.
- Maron, J.L., T. Potter, Y. Ortega, and D. Pearson. 2012. "Seed Size and Provenance Mediate the Impacts of Disturbance and Rodent Seed Predation on Community Assembly." *Journal of Ecology* 100: 1492–500.
- Maron, J.L., K.C. Baer, and A.L. Angert. 2014. "Disentangling the Drivers of Context-Dependent Plant–Animal Interactions." *Journal of Ecology* 102: 1485–96.
- Maron, J.L., K. Hajek, P. Hahn, and D.E. Pearson. 2018. "Rodent Seed Predators and a Dominant Grass Competitor Affect Coexistence of Co-Occurring Forb Species that Vary in Seed Size." *Journal of Ecology* 106: 1795–805.
- Maurer, G.E., A.J. Hallmark, R.F. Brown, O.E. Sala, and S.L. Collins. 2020. "Sensitivity of Primary Production to Precipitation across the United States." *Ecology Letters* 23: 527–36.
- M'Closkey, R.T. 1980. "Spatial Patterns in Sizes of Seeds Collected by Four Species of Heteromyid Rodents." *Ecology* 61: 486–9.
- Meserve, P.L., D.A. Kelt, B. Milstead, and J.R. Gutierrez. 2003. "Thirteen Years of Shifting Top-Down and Bottom-Up Control." *Bioscience* 53: 633–46.
- Mittlebach, G.G., and K.L. Gross. 1984. "Experimental Studies of Seed Predation in Old-Fields." *Oecologia* 65: 7–13.
- Moles, A.T., D.I. Warton, and M. Westoby. 2003. "Do Small-Seeded Species Have Higher Survival through Seed Predation than Large-Seeded Species?" *Ecology* 84: 3148–61.
- Moyano, J., M.C. Chiuffo, M.A. Nuñez, and M.A. Rodriguez-Cabal. 2019. "Seed Predation Does Not Explain Pine Invasion Success." *Oecologia* 189: 981–91.
- Muldavin, E.H., D.I. Moore, S.L. Collins, K.R. Wetherill, and D.C. Lightfoot. 2008. "Aboveground Net Primary Production Dynamics in a Northern Chihuahuan Desert Ecosystem." *Oecologia* 155: 123–32.
- Mulhouse, J.M., L.M. Hallett, and S.L. Collins. 2017. "The Influence of Seasonal Precipitation and Grass Competition on 20 Years of Forb Dynamics in Northern Chihuahuan Desert Grassland." *Journal of Vegetation Science* 28: 250–9.
- Munger, J.C., and J.H. Brown. 1980. "Competition in Desert Rodents: An Experiment with Semipermeable Exclosures." *Science* 211: 510–2.
- Nicolai, N. 2019. "Ecological engineers' Nests Benefit Plant Recovery Following Fire in a Semiarid Grassland, New Mexico, USA." *Journal of Vegetation Science* 30: 709–19.
- Noble, J.D. 2017. "Forage Selection and Habitat Architecture as Drivers of Small Mammal Community Dynamics in an Arid, Nutrient Limited, Highly Stochastic Ecosystem." PhD Dissertation. University of New Mexico, Albuquerque, NM. https://digitalrepository.unm.edu/biol_etds/252 (accessed March 2021).
- Noble, J.D., S.L. Collins, A.J. Hallmark, K. Maldonado, B.O. Wolf, and S.D. Newsome. 2019. "Foraging Strategies of Individual Silky Pocket Mice Over a Boom-Bust Cycle in a Stochastic Dryland Ecosystem." *Oecologia* 190: 569–78.
- Olf, H., and M.E. Ritchie. 1998. "Effects of Herbivores on Grassland Plant Diversity." *Trends in Ecology & Evolution* 13: 261–5.
- Orrock, J.L., D.T. Levey, B.J. Danielson, and E.I. Damschen. 2006. "Seed Predation, Not Seed Dispersal, Explains the Landscape-Level Abundance of an Early Successional Plant." *Ecology* 94: 838–45.
- Orrock, J.L., M.S. Witter, and O.J. Reichman. 2008. "Apparent Competition with an Exotic Plant Reduces Native Plant Establishment." *Ecology* 89: 1168–74.
- Pearson, D.E., R.M. Callaway, and J.L. Maron. 2011. "Biotic Resistance Via Granivory: Establishment by Invasive, Naturalized and Native Asters Reflects Generalist Preference." *Ecology* 92: 1748–57.
- Pearson, D.E., N.S. Icasatti, J.L. Hierro, and B.J. Bird. 2014. "Are Local Filters Blind to Provenance? Ant Seed Predation Suppresses Exotic Plants More than Natives." *PLoS One* 9: 1–11.
- Pearson, D.E., J.L. Hierro, M. Chiuffo, and D. Villarreal. 2014. "Rodent Seed Predation as a Biotic Filter Influencing Exotic Plant Abundance and Distribution." *Biological Invasions* 16: 1185–96.

- Petrie, M.D., S.L. Collins, D.S. Gutzler, and D.M. Moore. 2014. "Regional Trends and Local Variability in Monsoon Precipitation in the Northern Chihuahuan Desert, USA." *Journal of Arid Environments* 103: 63–70.
- Pinheiro, J., D. Bates, S. DebRoy, S. Hiesterkamp & B. Van Willigen. 2017. "Package 'nlme': Linear and Nonlinear Mixed Effects Models. v3.1-131."
- Pockman, W.T., and E.E. Small. 2010. "The Influence of Spatial Patterns of Soil Moisture on the Grass and Shrub Responses to a Summer Rainstorm in a Chihuahuan Desert Ecotone." *Ecosystems* 13: 511–25.
- Price, M., and K. Heinz. 1984. "Effects of Body Size, Seed Density, and Soil Characteristics on Rates of Seed Harvest by Heteromyid Rodents." *Oecologia* 61: 420–5.
- Price, M., and R. Podolsky. 1989. "Mechanisms of Seed Harvest by Heteromyid Rodents - Soil Texture Effects on Harvest Rate and Seed Size Selection." *Oecologia* 81: 267–73.
- Prugh, L.R., and J.S. Brashares. 2012. "Partitioning the Effects of an Ecosystem Engineer: Kangaroo Rats Control Community Structure Via Multiple Pathways." *Journal of Animal Ecology* 81: 667–78.
- R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Reader, R.J. 1993. "Control of Seedling Emergence by Ground Cover and Seed Predation in Relation to Seed Size for some Oldfield Species." *Journal of Ecology* 81: 169–75.
- Rudgers, J.A., Y. Anny Chung, G.E. Maurer, D.I. Moore, E.H. Muldavin, M.E. Litvak, and S.L. Collins. 2018. "Climate Sensitivity Functions and Net Primary Production: A Framework for Incorporating Climate Mean and Variability." *Ecology* 99: 578–82.
- Samson, D., T.D. Philippi, and D.W. Davidson. 1992. "Granivory and Competition as Determinants of Annual Plant Diversity in the Chihuahuan Desert." *Oikos* 65: 231–4.
- Schooley, R.L., B.T. Bestelmeyer, and A. Campanella. 2018. "Shrub Encroachment, Productivity Pulses, and Core-Transient Dynamics of Chihuahuan Desert Rodents." *Ecosphere* 9: e02330.
- Stapp, P., and G.A. Polis. 2003. "Influence of Pulsed Resources and Marine Subsidies on Insular Rodent Populations." *Oikos* 102: 111–23.
- Swartz, M.J., S.H. Jenkins, and N.A. Dochtermann. 2010. "Coexisting Desert Rodents Differ in Selection of Microhabitats for Cache Placement and Pilferage." *Journal of Mammalogy* 91: 1261–8.
- Thibault, K.M., S.K. Morgan Ernest, E.P. White, J.H. Brown, and J. R. Goheen. 2010. "Long-Term Insights into the Influence of Precipitation on Community Dynamics in Desert Rodents." *Journal of Mammalogy* 91: 787–97.
- Urban, M.C., P.L. Zarnetske, and D.K. Skelly. 2017. "Searching for Biotic Multipliers of Climate Change." *Integrative and Comparative Biology* 57: 134–47.
- Verdon, C. Danielle, and W. Stewart Franks. 2006. "Long-Term Behaviour of ENSO: Interactions with the PDO over the Past 400 Years Inferred from Paleoclimate Records." *Geophysical Research Letters* 33: L06712.
- Vicente-Serrano, S.M., S. Begueria, and J.I. Lopez-Moreno. 2010. "A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index." *Journal of Climate* 23: 1696–718.
- Werner, C.M., K.L. Stuble, A.M. Groves, and T.P. Young. 2020. "Year Effects: Inter-Annual Variation as a Driver of Community Assembly Dynamics." *Ecology* 00(00): e03104. <https://doi.org/10.1002/ecy.3104>
- Wickham, H. 2017. "tidyverse: Easily Install and Load the 'Tidyverse'." R package version 1.2.1. <https://CRAN.R-project.org/package=tidyverse> (accessed March 2021).
- Yeakel, J.D., U. Bhat, and S.D. Newsome. 2020. "Caching in or Falling Back at Sevilleta: The Effects of Body Size and Seasonal Uncertainty on Desert Rodent Foraging." *American Naturalist* 196: 241–56.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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