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Animals alter precipitation legacies: Trophic and ecosystem engineering effects on plant community temporal dynamics

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Abstract

1. Multiyear precipitation "legacies" can have stronger effects on plant community composition than rainfall in the current growing season, but variation in the magnitude of these effects is not fully understood. Direct interactions between plants and animals, such as herbivory, and indirect interactions, such as ecosystem engineering (via changes in the physical environment), may influence precipitation legacies by altering mechanisms of lagged effects. However, the role of direct and indirect plant–animal interactions in determining the strength of precipitation legacies remains largely unexplored.

2. Here, we investigated effects of current growing season rainfall and precipitation legacies on grassland composition, and the influence of herbivory and ecosystem engineering interactions on these temporal dynamics. From 2009 to 2014, a period spanning high and low rainfall, we recorded plant cover in kangaroo rat exclosures and paired control plots that included both burrow and inter-burrow areas. We used linear mixed effects modelling and analysis of community dissimilarities to evaluate plant composition responses to current and previous growing season rainfall and kangaroo rat herbivory (presence of seed foraging) and ecosystem engineering (burrowing).

3. We found that community composition was more strongly affected by precipitation legacies than by current growing season rainfall. Greater precipitation in the previous growing season enhanced grass cover and reduced forb and legume cover. Kangaroo rat trophic and engineering interactions had counteracting effects on these legacies. While burrowing increased grass cover and thereby amplified the effects of previous growing season rainfall on community composition, legacies were suppressed by the presence of kangaroo rat foraging, which decreased grass cover. Further analysis revealed that kangaroo rat foraging and burrowing had conflicting effects on residual plant biomass prior to the growing season, suggesting that precipitation legacies were influenced by altered litter dynamics.

4. *Synthesis*. Our study demonstrates that animals can impact the strength of precipitation legacies through direct and indirect interactions with the plant species that drive lag effects. The influence of multiple types of plant–animal interactions on precipitation legacies may be important to consider for ecosystem management and when generating predictions of community composition and productivity in future ecosystems.

1 | INTRODUCTION

Precipitation greatly affects plant productivity and composition across ecosystems (Hsu, Powell, & Adler, 2012) and is a primary driver of plant community dynamics in arid and semi-arid ecosystems (Noy-Meir, 1973; Webb, Lauenroth, Szarek, & Kinerson, 1983). Interestingly, current growing season rainfall is a strong predictor of variation in arid and semi-arid plant communities across space (Bai et al., 2008; McNaughton, 1985; Sala, Parton, Joyce, & Lauenroth, 1988) but is a relatively weak predictor of these same communities across time (Adler & Levine, 2007; Cleland et al., 2013; Sala, Gherardi, Reichmann, Jobbagy, & Peters, 2012). A growing consensus of studies now recognizes that precipitation in previous growing seasons can have a great effect on plant communities through time (Adler & Levine, 2007; Elmendorf & Harrison, 2009; Gibbens & Beck, 1988; Haddad, Tilman, & Knops, 2002; Lauenroth & Sala, 1992; Oesterheld, Loreti, Semmartin, & Sala, 2001; Reichmann & Sala, 2014; Sherry et al., 2008, 2012; Suttle, Thomsen, & Power, 2007); lag effects commonly referred to as "precipitation legacies" (Monger et al., 2015; Reichmann, Sala, & Peters, 2013; Sala et al., 2012). In grasslands dominated by perennial plants, much of the unexplained variance in relationships between current precipitation and primary production is related to precipitation legacies (Oesterheld et al., 2001; Reichmann et al., 2013; Sherry et al., 2008). Precipitation legacies also occur in annual grasslands, where they have been shown to have even greater effects on plant cover and composition than current growing season precipitation (Dudney et al., 2017; Hobbs & Mooney, 1995). It is therefore critical to consider precipitation legacies if we are to understand changes in plant communities through time; however, anticipating variation in the strength of these lag effects and recognizing their long-term repercussions remains a challenge.

The magnitude of precipitation legacies is determined by a variety of mostly plant-based mechanisms, including across-year changes in plant propagule and litter production, root resource storage, and soil properties, such as soil nutrient content, moisture, and the composition of micro-organisms (Haddad et al., 2002; Meisner, de Boer, Cornelissen, & van der Putten, 2012; Meisner, De Deyn, de Boer, & van der Putten, 2013; Reichmann & Sala, 2014; Reichmann et al., 2013; Sherry et al., 2008). Legacy strength depends on the amount of precipitation driving the lag mechanisms, but the magnitude of lagged effects may be altered by interactions between plants and animals that influence these mechanisms. For example, grazing can reduce litter and may suppress litter effects on the plant community in the following year (Dudney et al., 2017). In addition, grazing can remove plant reproductive structures and may affect precipitation-induced changes in the seed bank from which future communities arise (Dudney et al., 2017; Russi, Cocks, & Roberts, 1992). Non-trophic and indirect species interactions, such as ecosystem engineering (i.e. interactions mediated by physical ecosystem change: Hastings et al., 2007; Jones et al., 2010; Jones, Lawton, & Shachak, 1994), may also impact the strength of precipitation legacies. For instance, in a California grassland the cover of *Lasthenia californica* was highly correlated with precipitation in the previous year, and because *L. californica* cover was greater in the absence of gopher burrowing (Hobbs & Mooney, 1995), this legacy likely depends on soil engineering by gophers. Although multiple types of direct and indirect plant–animal interactions may increase variation in precipitation legacies, the influence of animals on these temporal dynamics has been little tested.

In this study, we evaluated effects of plant–animal trophic (direct consumption) and ecosystem engineering (indirect, environment-mediated) interactions on precipitation legacies in an annual grassland, the Carrizo Plain of California. Though less studied than perennial grasslands, precipitation in annual grasslands can create strong legacy effects on plant community composition that occurs through changes in seed and litter production (Dudney et al., 2017; Suttle et al., 2007). Greater rainfall in annual grasslands enhances the seed and litter production of grasses, which suppresses forb abundances and increases grass abundances the following year (Dudney et al., 2017). Legacies also occur when greater rainfall enhances legume growth, resulting in nitrogen-rich litter that decomposes and affects plants in following years (Suttle et al., 2007). We expected strong precipitation legacies in plant composition in our study system, and we further hypothesized that an abundant rodent, the giant kangaroo rat (*Dipodomys ingens*), would alter these legacies.

Giant kangaroo rats, hereafter referred to as "GKR," are granivores that dominate annual grasslands to the near exclusion of all other rodent species (Grinnell, 1932; Williams & Kilburn, 1991). Using a complex series of foraging behaviours, GKR seasonally collect and store seeds in large underground caches from which they derive nourishment throughout the year (Grinnell, 1932; Hawbecker, 1944; Shaw, 1934). These rodents may suppress precipitation legacies by diminishing seed abundances and preferentially foraging on seeds of plants responsible for lag effects, such as large-seeded grasses (Gurney, Prugh, & Brashares, 2015). Alternatively, GKR could strengthen precipitation legacies by enhancing the growth of plants that drive lag effects. For instance, GKR scatter-hoard seeds in temporary surface caches before moving them into their larders deep underground (Shaw, 1934). Though larder-hoards are too deep for seeds to germinate, unharvested surface caches could enhance germination of preferred grasses, similar to plant responses to scatter-hoarding by other kangaroo rat species (Reichman, 1979; Reynolds, 1950). Additionally, GKR foraging could cause weaker precipitation legacies by suppressing plant litter dynamics. Rather than wait for seeds to drop from plants, GKR clip plant stems and harvest whole seed heads (Hawbecker, 1944), which removes plant biomass (Prugh & Brashares, 2012) and may expedite litter decay. Altogether, GKR granivory could amplify or buffer the effects of precipitation legacies through multiple mechanisms.

In addition to trophic effects on plants, GKR may alter precipitation legacies indirectly by engineering large burrow systems that restructure soils and affect plants (Gurney et al., 2015). At the Carrizo Plain, GKR are distributed nearly continuously over hundreds of hectares, and their burrowing has a landscape-scale effect (Grinnell, 1932; Williams & Kilburn, 1991; photos in Bean, Stafford, Prugh, Butterfield, & Brashares, 2012; Gurney et al., 2015; Prugh & Brashares, 2012), as well as a patch-scale effect. These highly territorial rodents live singly within regularly spaced burrows that are maintained by successive generations (Braun, 1985; Cooper & Randall, 2007) and can potentially last for decades (Whitford & Kay, 1999). Locally, GKR burrows disturb patches of soil 7–10 m across, and there is a similar distance between burrows, resulting in the ground surface consisting of c. 50% burrow areas and 50% inter-burrow areas across the plain (Gurney et al., 2015). While burrow-driven changes in hydrology may affect soil properties over the landscape, at the patch scale kangaroo rat burrows have soils with lower water content and higher nutrient concentrations than areas between burrows (Greene & Reynard, 1932; Gurney et al., 2015; Moorhead, Fisher, & Whitford, 1988; Mun & Whitford, 1990). Precipitation legacies can potentially be affected by this soil engineering because burrows support greater grass growth than areas off burrows (Schiffman, 1994) and may result in stronger grass-driven precipitation legacies, especially within burrow patches. In contrast, legume growth is reduced on burrows compared to inter-burrow areas (Schiffman, 1994) and legacies resulting from legume litter may be expected to be weaker in the presence of burrowing. Thus, GKR ecosystem engineering interactions with plants could potentially increase or decrease the magnitude of precipitation legacies in grasslands.

To test whether GKR trophic and ecosystem engineering interactions amplify or suppress precipitation legacies, we conducted a manipulative field experiment over a 6-year period that included substantial variation in growing season rainfall. At each of 20 sites, we evaluated GKR trophic effects (i.e. granivory) by comparing plant communities in plots where GKR foraging was excluded to paired control plots where GKR foraging was unmanipulated. Within all plots, we compared plant communities on and off of burrows to evaluate GKR ecosystem engineering effects at the patch scale. Using plant cover data at the functional group and species levels, we examined community composition responses to rainfall in the current and previous growing seasons and the effects of GKR interactions on these dynamics. Furthermore, we evaluated the potential for litter production to mediate lag effects. To our knowledge, this study provides the first example of precipitation legacies being simultaneously altered by direct and indirect interactions between plants and animals.

2 | MATERIALS AND METHODS

2.1 | Study site and initial experimental design

We conducted our study in the Carrizo Plain National Monument in central California (USA), which contains the largest remaining GKR population. The Carrizo Plain is an arid grassland, composed primarily of annual plants, and is the largest remnant of the San Joaquin upland ecosystem that historically occurred throughout the Central Valley of California (Germano, Rathbun, & Saslaw, 2001). The climate is Mediterranean, with precipitation concentrated during cool winters, while summers are hot and dry. Total rainfall during the growing season (October to April) averaged 21.1 cm (range 7.0–52.5 cm) over the 20 years preceding and including our research (1995–2014; MesoWest CAZC1, 35.10N, 119.77W).

Our study experimentally measured trophic and burrow engineering interactions associated with the GKR (Prugh & Brashares, 2012). Trophic interactions were measured by comparing 20 replicate 400 m^2 kangaroo rat exclosures with paired unmanipulated plots located in a random compass direction 20 m from each GKR exclosure. Because GKR are the numerically (Grinnell, 1932) and behaviourally (Shaw, 1934) dominant small mammal in this ecosystem, we expected exclosures to primarily reflect changes in the presence of GKR and not other small mammals. We monitored the exclosures closely using observations and game cameras and did not see evidence of compensatory responses by other small mammals (e.g. ground squirrels), though other rodent species (and lizards) were observed climbing over exclosure barriers (Prugh & Brashares, 2012). If signs of kangaroo rat activity were present in an exclosure, these animals were immediately removed and tunnels leading into the exclosure were blocked. Here, we equate GKR presence with the presence of their foraging because we expected other mechanisms by which GKR presence may influence plants, such as dust bathing, to have weak effects by comparison.

We measured burrow engineering interactions by comparing burrow and inter-burrow areas both outside and within the exclosures. Burrows made up approximately half the area of each plot. The remarkably regular distribution and spacing of burrows indicate that burrow location was determined primarily by territoriality rather than microsite differences (Braun, 1985; Cooper & Randall, 2007). Additionally, burrows deteriorate slowly over many years (Hastings et al., 2007; Whitford & Kay, 1999) and were clearly identifiable in GKR exclosures after 6 years without burrow maintenance; thus, burrow engineering was little affected by the GKR foraging treatment. This is corroborated by prior results from this experiment showing that GKR presence did not influence effects of burrows on soil nutrients and other soil properties (Gurney et al., 2015). More recently, we have found that GKR burrowing effects on soil inorganic nitrogen, nitrogen mineralization and water content were unaffected by GKR presence, even after manipulating GKR presence for 8 years (J. G. Grinath, L. R. Prugh, J. S. Brashares, & K. N. Suding, unpubl. data). In general, burrows transitioned to inter-burrow areas (disturbed, mounded soil to undisturbed flat soil) within a 1-m span, and these edges were used to map the position of burrows in each experimental plot. We then randomly placed four 1 m² quadrats on burrows and four quadrats off burrows, in both the exclosure and unmanipulated plots (total = 320 quadrats). Quadrat placement on or off burrows was stable across years of our experiment, indicating that burrow location was stable within the landscape.

The GKR manipulations were established in 2008, and from 2009 to 2014 we measured plant cover in the experimental quadrats using pinframes (Prugh & Brashares, 2012). At peak primary production in April, frames were placed over vegetation and a pin was dropped at each of 81 points spaced at 10 cm intervals throughout the frame. The species identity of the first vegetation encountered by each pin drop was recorded as a "hit"; we also recorded the presence of plants within the 1 m² sampling area that were not hit by a pin. Each pin hit corresponds with plant cover, and to include data for rare or short species not hit by a pin, we considered the presence of a plant species as an additional hit. Thus, each species' cover was based on a total of 82 potential hits, each hit equalling 1.22% cover. In addition, in October of each year, we measured residual aboveground dry plant biomass in a 1/16 m² area adjacent to all experimental quadrats. We also measured unvegetated litter cover during the April plant species cover surveys; this variable represents litter bare of living plants.

To understand the effects of our GKR manipulations, we monitored the densities of GKR and other rodents from 2007 to 2014. In April and August of each year, nocturnal rodent density was estimated using three to five night mark–recapture sessions at each of the 20 study sites. Sherman traps were arranged in a 1-ha trapping grid (n = 60 traps) encompassing the experimental plots at each site (traps were not set within GKR exclosures, which were monitored with game cameras). All captured rodents were marked with PIT and ear tags, and released. We estimated diurnal rodent (i.e. squirrel) density over the same trapping grids using 5-day mark–recapture sessions in May of each year. These rodents were captured using

Tomahawk traps, and each individual was marked with a PIT tag, and released. To estimate rodent densities, robust design capture–recapture models were implemented with the RMark package in R 3.2.3 (R Core Team, 2015).

2.2 | Statistical analyses

We first investigated patterns in plant functional group responses to precipitation regardless of GKR, then we examined how GKR interactions with plants influenced rainfall effects on functional and species composition. All statistical analyses were conducted in R 3.2.3 (R Core Team, 2015). Prior to analysis, plant cover was checked to identify extremely rare species that may have skewed the results (McCune & Grace, 2002). We removed all species that had less than 0.0001 relative cover across all the raw data or that occurred in fewer than 4 years of study. With the data thus filtered, we calculated species relative cover and functional group relative cover to measure community and functional composition, respectively. We also excluded quadrats if it was unclear whether they occurred off or on a burrow (i.e. if quadrats spanned the edge of these areas). In total, the data used for this analysis included 1,782 observations of plant communities from 297 quadrats.

For our initial evaluation of plant community responses to precipitation, we analysed the relative cover of each of the three functional groups: non-leguminous forbs (hereafter "forbs"), grasses and legumes. We used repeated measures linear mixed effects models (RM-LMMs; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) based on quadrat data within plots. We performed models for unbalanced data using the "lme" function from the package NLME, with type II SS using the "ANOVA" function from the package CAR. To account for spatial autocorrelations and the repeated measures design, we included random intercept terms for quadrat grouped within plot, grouped within site. Though quadrats were placed off and on GKR burrows, quadrats within plots were not spatially clustered by this factor (the nearest neighbour of many quadrats was in the opposite treatment), and we did not include this as an additional grouping factor. To account for temporal effects across years, we included a continuous temporal autocorrelation term, corCAR1, in the models (year rescaled as a vector from 0 to 5), which is robust to missing data. Precipitation in the current and previous growing season were included as continuous predictor variables in the RM-LMMs; we also considered the interaction between these explanatory variables.

To account for violations of equal variance of the residuals in our models, we performed a model selection procedure to find the optimal variance structure for each model (Zuur et al., 2009). We did not perform model selection on fixed variables because we were interested in comparing models for each plant functional group that had equivalent fixed explanatory structure, which was determined a priori. We fit models with seven different variance structures (none; fixed, power or exponential structures for current or previous rainfall), and selected the best model based on lowest Akaike information criterion (AIC) values and evaluation of the residuals. Preliminary assessment of the relative cover data indicated that a transformation

was necessary to achieve normality in the models; therefore, we ln(x + 1) transformed the data prior to analysis. If needed to further meet assumptions of normality in the models, we removed up to five extreme outlying data points (out of 1,782 observations) that were likely due to measurement error (Zuur et al., 2009).

Next, we analysed how community composition at the species level responded to precipitation and GKR interactions. Using Bray–Curtis dissimilarities calculated from species relative cover data, we performed a permutational multivariate ANOVA (PerMANOVA) to evaluate the significance of plant compositional responses, and we visualized these effects using non-metric multidimensional scaling (NMDS). The PerMANOVA was performed using the "adonis" function (999 iterations) from the package "vegan." Though plant cover data were collected at the scale of quadrats grouped within plots (400 m^2 sampling areas), grouped within sites, only two hierarchical levels can be used in the PerMANOVA. To meet this data requirement, we averaged across quadrat-level data to obtain four mean plant communities for each site, corresponding with the GKR experimental treatments (off burrow/foraging absent, off burrow/foraging present, on burrow/foraging absent, on burrow/foraging present). These data were calculated for every site in all 6 years of study, yielding a data frame with 480 communities. Dissimilarities calculated from this data were evaluated as a function of precipitation in the current growing season, precipitation in the previous growing season, GKR foraging, GKR burrowing, and all interactions among these explanatory factors (terms added sequentially). Kangaroo rat interactions were entered as binary factors. The additive effect of site was included as a grouping variable, as was year to account for the repeated measures experimental design.

After conducting the PerMANOVA, we used NMDS to illustrate the effects of precipitation and GKR on plant community dissimilarities. NMDS is a descriptive statistical technique that represents community dissimilarities in a specified number of dimensions. With the same data that were used in the PerMANOVA, we performed a two-dimensional NMDS using the "metaMDS" function from the "vegan" package. We fit the precipitation and GKR explanatory variables to the NMDS to further understand their influence on community composition. Rainfall in the current and previous growing season were fit as surfaces and represented with contour maps within the NMDS. To evaluate the potential for synergies between precipitation in the current and previous year, we included a variable representing their multiplicative effect (precipitation in the current year multiplied by that in the previous year), which we fit to the NMDS as a vector. We depicted differences in community space occupied by the GKR treatments by drawing ellipses (1SD) around centroids for each treatment level.

To understand which species caused differences in community composition over the GKR treatments, we used indicator species analyses (Dufrene & Legendre, 1997). These analyses calculate each species' indicator value across treatment levels based on species fidelity and relative abundances (or cover). We used permutation tests implemented with the function "indval" from the "labdsv" package to evaluate when species were significant indicators of

GKR experimental treatments. To better relate these analyses to our community dissimilarity results, we calculated indicator species values using the same data as in the PerMANOVA and NMDS.

Following the species-level analysis, we investigated mechanisms leading to plant compositional changes. First, we evaluated how relative cover responses were driven by changes in absolute plant cover, focusing on the three plant functional groups (forbs, grasses and legumes). We analysed each functional group with the same RM-LMM procedure described above, with a few modifications. Precipitation in the current and previous growing season was each included as continuous variables in the RM-LMMs, and GKR foraging and burrowing were included as binary factors. We also considered all possible interactions among these four explanatory variables, which was our a priori fixed variable structure. To find the optimal variance structure to account for unequal variances of the residuals, we fit models with 10 different variance structures (none; identity structure for GKR foraging, burrowing and their combination, and fixed, power or exponential structures for current or previous rainfall), and selected the best model based on lowest AIC values and evaluation of the residuals. Preliminary assessment indicated that a transformation was necessary to achieve normality in the models; therefore, we ln(x + 1) transformed the data prior to analysis.

Lastly, we investigated the potential for precipitation legacies to occur through litter production (Dudney et al., 2017). To investigate whether litter could have driven lag effects in our system, we evaluated responses of October residual above-ground biomass to precipitation and GKR using the RM-LMM procedure described above for absolute plant responses (Tukey post hoc contrasts evaluated with the "multcomp" package). We used linear regression to relate October litter to the cover of unvegetated litter the following spring (representing litter exclusive of living plant cover). We then examined unvegetated litter cover responses to precipitation using the same RM-LMM procedure described for functional group relative cover responses.

3 | RESULTS

3.1 | Temporal trends in rainfall and rodents

From 2007 to 2014, growing season precipitation at the Carrizo Plain was 17.4 cm on average and ranged from 7.0 to 39.7 cm (Figure 1). Rainfall was less than the 20 year mean, 21.1 cm, in all but two consecutive years, in which precipitation was much higher. In all years, GKR were the most abundant rodent species, and in some years, GKR were an order of magnitude more numerous than all other rodents combined (Figure 1). GKR initially increased in abundance from 2007 to 2008, and then maintained high densities until 2014, when GKR densities plummeted and were similar to those of all other rodents combined. Despite this variability, these trends confirm that the rodent exclosures primarily manipulated GKR foraging, because GKR abundances were high in all years preceding plant surveys (2008–2013). Of the other rodents, 97% were San Joaquin antelope squirrels (*Ammospermophilus nelsoni*), 2% were short-nosed kangaroo
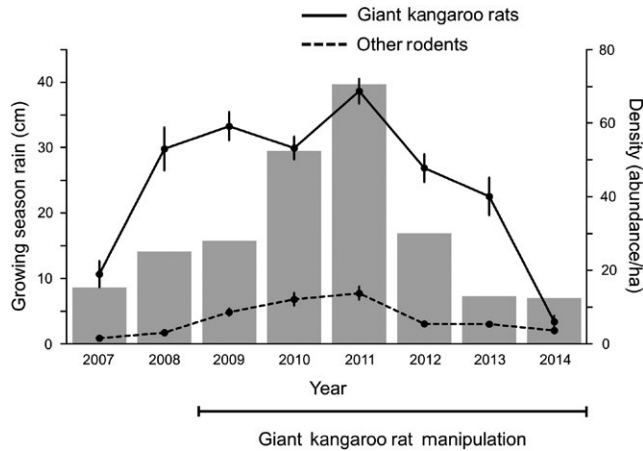
FIGURE 1 Growing season precipitation and rodent densities from 2007 to 2014 at the Carrizo Plain, California. Rainfall during the growing season (grey bars) was calculated as total precipitation from October to April (year corresponds with April). Densities of giant kangaroo rats and other rodents are shown as $M \pm 1SE$. Kangaroo rat exclosures were installed in 2008 and plant responses were recorded from 2009 to 2014, indicated along the *x*-axis

rats (*Dipodomys nitratoides brevinasus*), and the remaining 1% were California ground squirrels (*Otospermophilus beecheyi*), deer mice (*Peromyscus maniculatus*), southern grasshopper mice (*Onychomys torridus*), and Heermann's kangaroo rats (*Dipodomys heermanni*).

3.2 | Plant community composition responses

Plant functional composition responded more strongly to precipitation legacies than to rainfall in the current growing season (Figure 2, Table S1). Non-leguminous forbs had a weak negative relative cover response to current growing season rainfall ($\chi^2 = 7.74$, $p = .005$), and a much stronger negative response to precipitation in the previous growing season (Figure 2a; $\chi^2 = 558.35$, $p < .001$). Conversely, grass relative cover had a much greater positive response to previous than current growing season rainfall, and an interactive effect resulted in grasses having greater relative cover when previous year rainfall was high but current precipitation was low (Figure 2b; two-way interaction: $\chi^2 = 23.81$, $p < .001$). This interactive effect corresponded with legume relative cover, which was low in all conditions but decreased further when previous growing season rainfall was high and that of the current year was low (Figure 2c; two-way interaction: $\chi^2 = 28.41$, $p < .001$).

At the species level, GKR trophic and engineering interactions both altered community composition responses to precipitation legacies. Using PerMANOVA (Table 1), we found that current and previous growing season rainfall had interactive effects on community composition. These effects were influenced by GKR burrowing (significant three-way interaction) and by GKR foraging (significant two-way interactions).

To examine the nature of these interactive effects on species composition, we used NMDS to map community dissimilarities in two-dimensional ordination space. Figure 3a shows the position
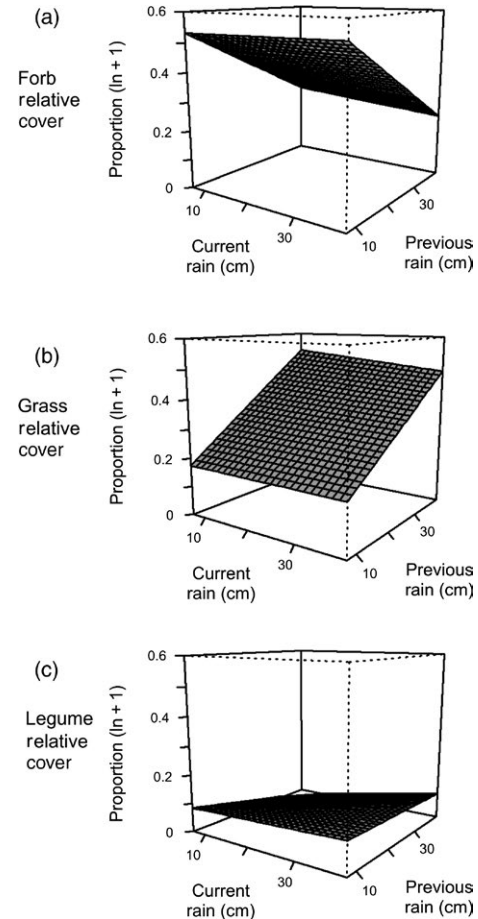

FIGURE 2 Functional composition response to precipitation in the current and previous growing season. The community was composed of (a) non-leguminous forbs, (b) grasses and (c) legumes. Functional group cover was relativized to evaluate compositional changes, and relationships with rainfall are visualized as average response surfaces

of each plant species in ordination space; Table 2 contains a corresponding species list (with plant identification codes). Most species were clustered in the centre of the NMDS and overlapped with other species. The sole exception was *Hordeum murinum* (G4), an exotic grass that was alone in ordination space, indicating that this species had a large effect on community composition. The position of this species aligns with greater precipitation in the previous growing season (dark blue contours) and the multiplicative effect of rainfall across years (red arrow) shown in Figure 3b. Other species with greater representation due to precipitation legacies included the grasses *Bromus madritensis* ssp. *rubens* (G1), *Festuca myuros* v. *hirsuta* (G3) and *Festuca microstachys* v. *pauciflora* (G2). Communities shifted towards lower composition by these grass species in the presence of GKR foraging, which suppressed the influence of precipitation in the previous and current growing seasons (Figure 3c: ellipses). In contrast, burrowing amplified grass representation in the community, particularly as greater rainfall in both the current and previous growing seasons favoured *H. murinum* and *B. madritensis* ssp. *rubens* (Figure 3d: ellipses).

TABLE 1 Permutational multivariate analysis of variance (PerMANOVA) results for the effects of precipitation and giant kangaroo rat experimental treatments on plant community dissimilarities (Bray–Curtis). Explanatory variables included rainfall in the current or previous growing season and kangaroo rat foraging and burrowing; we also considered statistical interactions among these factors. Site and year were included as grouping variables to account for multiple observations at each site through time

Explanatory variable	df	F	R^2	p
Foraging (F)	1	34.680	.032	.001
Burrowing (B)	1	48.954	.046	.001
Current rain (C)	1	59.020	.055	.001
Previous rain (P)	1	86.160	.080	.001
Year	1	28.412	.026	.001
Site	19	16.958	.299	.001
F × B	1	2.640	.002	.010
F × C	1	6.075	.006	.001
B × C	1	2.038	.002	.042
F × P	1	9.711	.009	.001
B × P	1	14.960	.014	.001
C × P	1	11.788	.011	.001
F × B × C	1	0.222	0	.987
F × B × P	1	1.112	.001	.356
F × C × P	1	1.852	.002	.080
B × C × P	1	2.074	.002	.030
F × B × C × P	1	0.441	0	.904
Residuals	444			.413

We used indicator species analyses to better understand which species characterized communities under each GKR treatment. Species that were significant indicators in each GKR condition are shown in Table 2 (indicator values in Table S2), along with each species' average relative cover. The grasses *H. murinum* and *B. madritensis* ssp. *rubens* had the highest of all indicator values and characterized communities occurring on burrows in the absence of GKR foraging; another grass, *Schismus arabicus*, had the next highest indicator value and occurred mainly on burrows when GKR were present. Yet different grass species were indicators off burrows in the presence and absence of GKR foraging. Many forb species were indicators, especially off burrows and in the presence of GKR foraging, but forbs and legumes had relatively low indicator values compared to grasses (Table S2). These results show that GKR trophic and ecosystem engineering interactions primarily affected grasses over species in other functional groups.

3.3 | Mechanisms of compositional responses

We next evaluated how changes in plant composition (i.e. relative cover) were driven by changes in absolute plant cover, focusing on plant functional group responses (Figure 4, Table S3). Across all GKR treatments, forb absolute cover increased as current growing season
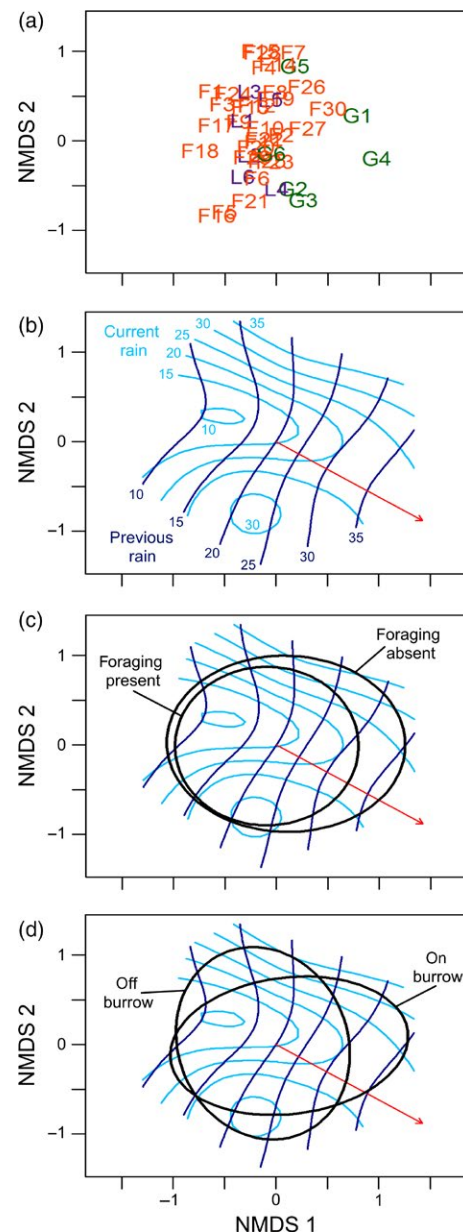

FIGURE 3 Non-metric multidimensional scaling (NMDS) of species-level plant community composition. Bray–Curtis dissimilarities were calculated across experimental treatments and years and mapped onto two dimensions (stress = 0.259). In (a), plant species are shown with codes corresponding to functional groups, with forbs = F1 to F30 (orange), grasses = G1 to G6 (green) and legumes = L1 to L6 (purple); full species names are provided in Table 2. In (b–d), explanatory variables were fit to the NMDS. Contours representing rainfall in the current (light blue) or previous (dark blue) growing season are provided in (b), along with a vector for the multiplicative effect of precipitation across years (red arrow). In (c) and (d), community differences in the kangaroo rat experimental treatments are shown with ellipses (1*SD*) drawn around centroids for each treatment level. The colour version of this figure can be found in the online article

precipitation increased, except when precipitation in the previous growing season was high. Kangaroo rat foraging suppressed this

TABLE 2 Plant species list with functional group designations and relative cover across the giant kangaroo rat experimental treatments. Most species have annual life histories and are native to California; perennial plants (p) and those of exotic origin (e) are designated following species names. Significant indicator species ($p \leq .05$) are shown with the cover value in bold for the experimental treatment they represent. Relative cover was averaged over 2009–2014

Plant ID	Scientific name	Family	Foraging absent		Foraging present	
			Off burrow	On burrow	Off burrow	On burrow
Forbs						
F1	Allium sp. (p)	Alliaceae	0.0015	0.0007	0.0015	0.0006
F2	*Amsinckia tessellata*	Boraginaceae	0.0057	0.0397	0.0064	**0.0537**
F3	Calandrinia menziesii	Montiaceae	0.0257	0.0281	0.0425	0.0374
F4	*Camissonia campestris*	Onagraceae	**0.0007**	0.0001	0.0004	0.0001
F5	*Capsella bursa-pastoris* (e)	Brassicaceae	0.0000	0.0000	0.0002	**0.0003**
F6	*Caulanthus lasiophyllus*	Brassicaceae	0.0004	**0.0046**	0.0004	0.0035
F7	Chaenactis glabriuscula v. glabriuscula	Asteraceae	0.0058	0.0049	0.0015	0.0035
F8	*Chorizanthe uniaristata*	Polygonaceae	0.0087	0.0024	**0.0094**	0.0034
F9	*Dichelostemma capitatum* (p)	Themidaceae	**0.0202**	0.0108	0.0171	0.0086
F10	Eriogonum gracillimum	Polygonaceae	0.0071	0.0105	0.0123	0.0113
F11	Erodium cicutarium (e)	Geraniaceae	0.2758	0.2499	0.2819	0.2569
F12	*Herniaria hirsuta ssp. cineria* (e)	Caryophyllaceae	0.0034	0.0016	**0.0050**	0.0018
F13	*Hollisteria lanata*	Polygonaceae	0.0073	0.0039	**0.0130**	0.0076
F14	*Lastarriaea coriacea*	Polygonaceae	**0.0433**	0.0162	0.0333	0.0159
F15	*Lasthenia californica*	Asteraceae	**0.0070**	0.0017	0.0017	0.0012
F16	Lasthenia minor	Asteraceae	0.0187	0.0206	0.0155	0.0223
F17	Lepidium dictyotum	Brassicaceae	0.0017	0.0013	0.0027	0.0012
F18	Lepidium nitidum	Brassicaceae	0.0587	0.0513	0.0574	0.0613
F19	*Leptosiphon liniflorus*	Polemoniaceae	**0.0115**	0.0031	0.0073	0.0020
F20	Malacothrix coulteri	Asteraceae	0.0003	0.0002	0.0002	0.0003
F21	Microseris douglasii	Asteraceae	0.0062	0.0040	0.0033	0.0029
F22	*Microseris elegans*	Asteraceae	0.0065	0.0036	**0.0093**	0.0051
F23	Microsteris gracilis	Polemoniaceae	0.0006	0.0001	0.0004	0.0005
F24	*Pectocarya penicillata*	Boraginaceae	0.0171	0.0084	**0.0339**	0.0162
F25	Plagiobothrys canescens	Boraginaceae	0.0002	0.0003	0.0028	0.0013
F26	Plantago erecta	Plantaginaceae	0.0031	0.0009	0.0038	0.0013
F27	Stephanomeria pauciflora (p)	Asteraceae	0.0003	0.0008	0.0003	0.0010
F28	*Tetrapteron palmeri*	Onagraceae	0.0001	0.0000	**0.0008**	0.0001

(Continues)

TABLE 2 (Continued)

Plant ID	Scientific name	Family	Foraging absent		Foraging present	
			Off burrow	On burrow	Off burrow	On burrow
F29	*Tropidocarpum gracile*	Brassicaceae	0.0053	0.0067	0.0104	0.0082
F30	*Uropappus lindleyi*	Asteraceae	0.0007	0.0020	0.0005	0.0014
		Total forbs	0.5434	0.4788	0.5754	0.5307
Grasses						
G1	*Bromus madritensis ssp. rubens (e)*	Poaceae	0.0853	**0.1775**	0.0303	0.0895
G2	*Festuca microstachys v. pauciflora*	Poaceae	**0.1375**	0.0884	0.1056	0.0834
G3	*Festuca myuros v. hirsuta (e)*	Poaceae	0.0149	0.0064	0.0111	0.0053
G4	*Hordeum murinum (e)*	Poaceae	0.0233	**0.1412**	0.0050	0.0613
G5	*Poa secunda ssp. secunda (p)*	Poaceae	0.0344	0.0093	**0.0475**	0.0232
G6	*Schismus arabicus (e)*	Poaceae	0.0512	0.0444	0.1262	**0.1505**
		Total grasses	0.3466	0.4672	0.3258	0.4131
Legumes						
L1	*Acmispon wrangelianus*	Fabaceae	**0.0353**	0.0160	0.0237	0.0162
L2	*Astragalus didymocarpus*	Fabaceae	0.0005	0.0002	0.0003	0.0003
L3	*Astragalus lentiginosus v. nigricalycis (p)*	Fabaceae	0.0047	0.0024	0.0021	0.0006
L4	*Astragalus oxyphysus (p)*	Fabaceae	0.0085	0.0048	0.0135	0.0014
L5	*Lupinus microcarpus v. microcarpus*	Fabaceae	0.0026	0.0026	0.0006	0.0012
L6	*Trifolium gracilentum*	Fabaceae	0.0585	0.0281	0.0586	0.0365
		Total legumes	0.1100	0.0540	0.0988	0.0562

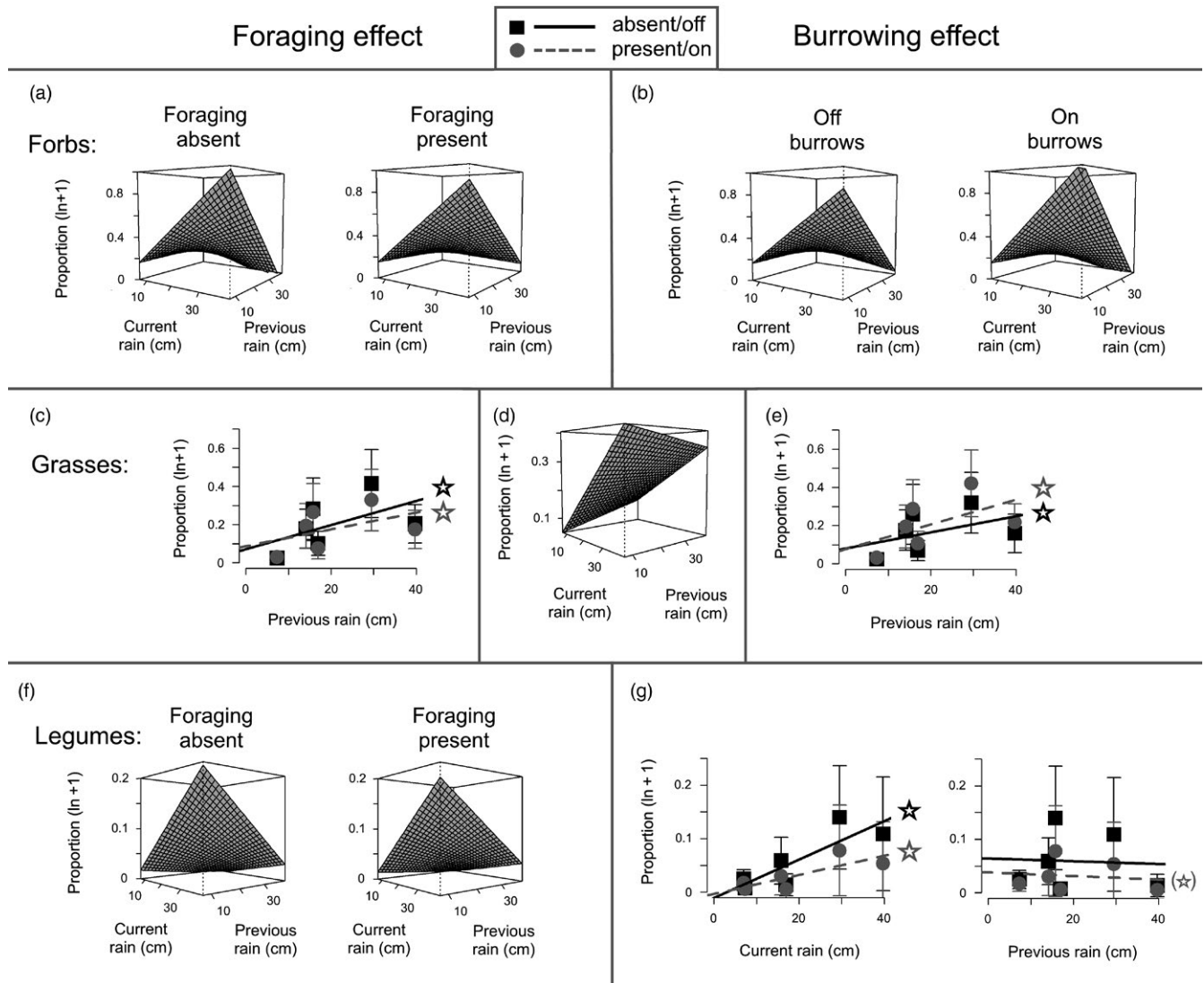## Absolute plant cover responses

FIGURE 4 (a, b) Forb, (c–e) grass and (f, g) legume absolute cover responses to precipitation and giant kangaroo rats. Responses to kangaroo rat (a, c, f) foraging and (b, e, g) burrowing are in the left and right columns, respectively, with (d) independent rainfall effects in the centre. Statistical interactions between rain in the current and previous growing season are visualized as average response surfaces. When current and previous rainfall had effects that were independent of each other, data are shown as $M \pm 1SD$ for each year. Average conditions are shown as simple post hoc regressions calculated using all the data; regressions with stars are significant ($p \leq .05$), or marginally significant ($p \leq .10$, denoted by parentheses)

lagged effect (Figure 4a; three-way interaction: $\chi^2 = 22.33$, $p < .001$), while GKR burrowing amplified this effect (Figure 4b; three-way interaction: $\chi^2 = 10.41$, $p = .001$).

Grass absolute cover increased with greater rain in the current growing season and maintained high cover the year after there was high rainfall (Figure 4d; two-way interaction: $\chi^2 = 113.54$, $p < .001$). Kangaroo rat foraging weakened the response to previous year precipitation, resulting in lower grass cover (Figure 4c; two-way interaction: $\chi^2 = 9.17$, $p = .002$). Kangaroo rat burrowing had the opposite effect, increasing the strength of response to previous growing season rainfall and causing greater grass cover (Figure 4e; two-way interaction: $\chi^2 = 16.17$, $p < .001$).

Similar to non-leguminous forbs, legume absolute cover increased with greater precipitation in the current year, but not when previous growing season rainfall was high (Figure 4). Unlike forbs, legume cover decreased further when current year rainfall was low and that in the previous year was high. These responses were weakened by GKR foraging (Figure 4f; three-way interaction: $\chi^2 = 5.07$, $p = .024$). Current rainfall effects were also weaker in the presence of GKR burrowing (Figure 4g; two-way interaction: $\chi^2 = 69.67$, $p < .001$), but burrowing tended to strengthen legacy effects on legume cover (two-way interaction: $\chi^2 = 24.22$, $p < .001$). In sum, these results indicate that strong responses of absolute grass cover to current growing season rainfall drove changes in community composition across years.

Lastly, we investigated whether litter dynamics could have been responsible for the precipitation legacies. Residual biomass in Fall prior to the next growing season (i.e. litter) increased with greater current growing season precipitation and, regardless of current rainfall, was abundant when rainfall in the previous year was high (Figure 5a, Table S3; two-way interaction: $\chi^2 = 15.21$, $p < .001$). Residual biomass also responded to both GKR foraging and burrowing (Figure 5b; two-way interaction: $\chi^2 = 9.07$, $p = .003$). Kangaroo rat foraging decreased residual biomass, while burrowing increased residual biomass, and these effects offset each other. Unvegetated litter cover (i.e. litter bare of living plants) in Spring at the end of the growing season was positively related to residual biomass prior to the growing season (Figure 5c; ln-litter cover = 0.096 × ln-residual biomass + 0.059: $t = 22.86$, $p < .001$, $R^2 = .26$). This litter cover decreased as precipitation in the current growing season increased, but only when there was low rainfall in the previous growing season (Figure 5d, Table S1; two-way interaction: $\chi^2 = 162.67$, $p < .001$). At all levels of current rainfall, unvegetated litter cover became greater as previous growing season rainfall increased. Together, these results indicate that forb and legume responses to current rainfall were inhibited by litter produced in the previous growing season.

4 | DISCUSSION

Our study shows that the composition of an annual grassland was more strongly controlled by precipitation in the previous growing season than that in the current year, and animals altered these dynamics. When there was low precipitation in the previous growing season, greater rainfall in the current year increased the absolute cover of all plant functional groups and there was little change in functional composition. However, functional composition following a high rainfall year was much different as plants responded to precipitation legacies. Grasses produce litter that is highly persistent compared to forbs (Dudney et al., 2017; Pitt & Heady, 1978). Our results indicate that increases in grass cover enhanced litter that suppressed forb and legume growth in the next growing season, whereas grass growth was unaffected by litter (Bartolome et al., 2007). There was no evidence for lag effects occurring via legume litter production (Suttle et al., 2007). These grass-driven lag dynamics resulted in a community with greater grass and lower forb and legume composition.

The magnitude of precipitation legacies depended on the trophic and ecosystem engineering effects of animals on grass cover and litter. Kangaroo rat foraging decreased grass cover and suppressed precipitation legacies. On the other hand, GKR burrowing increased grass cover, causing legacies to intensify. We did not find interactive effects of GKR foraging and burrowing on functional group cover, indicating that plant responses were additive; and because the effects were similar in magnitude and counteracting, GKR had little net effect on functional group composition in this grassland. Moreover, we found that GKR foraging and burrowing had an interactive effect on litter production that suggests these interactions had offsetting effects on the mechanism underlying the precipitation legacies. Though GKR foraging and burrowing had different magnitudes of effect on litter production, their combined influence was neutral compared to areas without foraging and off burrows. These results demonstrate the importance of considering multiple types of interactions for understanding the net effect of organisms on ecological communities. Our factorial experimental design was able to partition the effects of direct trophic and indirect ecosystem engineering interactions on a plant community, whereas experiments assessing these interactions individually may have come to opposite conclusions about the effects of GKR on plant communities. Ecological networks commonly contain multiple types of direct and indirect species interactions (Ings et al., 2009), and trophic and ecosystem engineering interactions must be considered together in the same ecological web to gain a more realistic understanding of ecological dynamics (Prugh & Brashares, 2012; Sanders et al., 2014; Wilby, Shachak, & Boeken, 2001).

While the trophic and ecosystem engineering interactions had a net neutral effect on plant functional composition, these
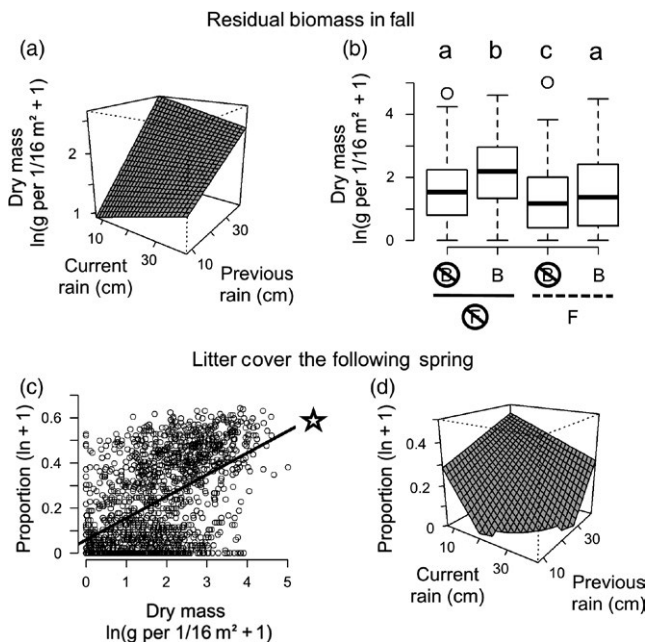

FIGURE 5 Fall residual biomass and unvegetated Spring litter cover responses. Dry above-ground biomass was measured in October, prior to the start of the next growing season, and was affected by both (a) rainfall and (b) rodents. Litter cover was only measured if no living vegetation occurred above the litter. (c) Greater residual biomass resulted in higher unvegetated litter cover the following April. (d) Unvegetated litter cover was dependent on rainfall in both the current and previous growing seasons. Kangaroo rat experimental factors are indicated under boxplots: F = foraging, and B = burrowing. Symbols with crosses represent control conditions (foraging absent or off burrow), while those without crosses are contrasting treatment conditions. To interpret two-way statistical interactions, lowercase letters above boxplots represent significant post hoc contrasts ($p \le .05$). The star next to the regression in (c) also indicates significance

interactions combined to alter species-level community composition within functional groups. Legacy effects were driven by exotic species that dominated the grass assemblage and were greatly influenced by kangaroo rats. In particular, *H. murinum*, and to a lesser extent *B. madritensis* ssp. *rubens*, had strong responses to rainfall in the previous growing season. These exotic species also increased on GKR burrows but decreased in the presence of GKR foraging, making way for another exotic species (*S. arabicus*) to dominate the grass assemblage on burrows. Like many grasslands throughout the world (D'Antonio & Vitousek, 1992), California grasslands are highly invaded by annual grasses of European origin (Jackson, 1985) that have displaced native vegetation (DiVittorio, Corbin, & D'Antonio, 2007; HilleRisLambers, Yelenik, Colman, & Levine, 2010). Native plant species still persist in many California grasslands (Levine & Rees, 2004), but it may only be a matter of time before they are driven locally extinct (Gilbert & Levine, 2013). Understanding variability in precipitation legacy effects on shifts in species composition may be key to conserving native plants in the wake of these invasions.

Careful management of direct and indirect plant–animal interactions may be used to control precipitation legacies and their unwanted repercussions. For instance, although livestock grazing may have led to grass invasions in California (HilleRisLambers et al., 2010), grazing can reduce grass and litter production and enhance the growth of native species (Hayes & Holl, 2003; Stahlheber & D'Antonio, 2013). Thus, greater livestock grazing in wet years can be used to reduce precipitation legacies (Dudney et al., 2017) and promote native species persistence in following years. In our study system, GKR foraging can remove more plant biomass than cattle (Endicott, Prugh, & Brashares, 2011). This foraging resulted in greater cover for many native forb species that otherwise would have been suppressed by exotic grass-driven legacies. Moreover, GKR foraging benefitted the grass *Poa secunda* ssp. *secunda*, a native perennial species that is frequently used in ecological restoration (Shaw & Mummey, 2017) but is negatively affected by invasive grasses (Herget, Hufford, Mummey, Mealor, & Shreading, 2015; Herget, Hufford, Mummey, & Shreading, 2015). The persistence of these species may rely on continued management to conserve GKR populations and their trophic interactions.

Giant kangaroo rats are the dominant rodent at the Carrizo Plain, but they are endangered globally (Williams & Kilburn, 1991). World-wide, burrowing rodents are experiencing population declines (Davidson, Detling, & Brown, 2012) and their ecological impacts are deteriorating in concert. Rodent foraging helps to maintain diverse grasslands (Brown & Heske, 1990; Ceballos et al., 2010; Curtin, Kelt, Frey, & Brown, 1999; Ponce-Guevara, Davidson, Sierra-Corona, & Ceballos, 2016; Weltzin, Archer, & Heitschmidt, 1997), and their ecosystem engineering interactions due to burrowing are also influential for plant communities. Across rodent species, burrows have different soil properties than surrounding areas (Ayarbe & Kieft, 2000; Greene & Reynard, 1932; Gurney et al., 2015; Kerley, Whitford, & Kay, 2004; Laundre, 1993; Moorhead et al., 1988; Mun & Whitford, 1990) and support different plant communities than habitats off

burrows (reviewed in Huntly & Inouye, 1988; Huntly & Reichman, 1994; Reichman & Seabloom, 2002; Whitford & Kay, 1999). Our study demonstrates that the promotion of precipitation legacies is one way in which rodent burrowing influences plant community composition. Though GKR burrowing enhanced the lag effects of exotic grasses, burrows also supported greater growth of some native forbs (*Amsinckia tessellata* and *Caulanthus lasiophyllus*). In addition, this engineering amplification of precipitation legacies may be desirable in some cases; for example, if the management goal is to increase forage production and quality for grazing (Hawbecker, 1944). Furthermore, our study focused on patches of grassland on and off burrows within the broader landscape, but GKR burrowing transforms entire landscapes (Bean et al., 2012; Grinnell, 1932; Gurney et al., 2015; Prugh & Brashares, 2012; Williams & Kilburn, 1991), the implications of which deserve further study. Because burrowing rodents can affect precipitation legacies in multiple ways through direct and indirect interactions, these species must be conservation priorities if we are to manage the lagged effects of precipitation on grassland communities.

The present study also suggests that conservation efforts for GKR and other burrowing rodents may become more challenging as climate change ensues. Though the Carrizo Plain contains the largest remaining population of GKR, we found that this population undergoes extreme fluctuations that could potentially increase the species' vulnerability to extinction. Abundances of GKR crashed in the last year of our study following two consecutive years of very low rainfall, which was the most severe drought in California in the last millennium (Griffin & Anchukaitis, 2014). The GKR population was resistant to the first year of drought, perhaps because seed hoards buffered the effects of low seed production, but was vulnerable to extended drought. Climate change is expected to result in greater aridity in this region (Cayan, Maurer, Dettinger, Tyree, & Hayhoe, 2008; Seager et al., 2007), which could adversely affect the GKR and its ecological role in the community. While this population crash could have dampened the magnitude of GKR foraging effects in the results shown here, our results were primarily influenced by the GKR population in the preceding year. Plant responses were measured prior to seed harvest by GKR in the present year and the GKR population crash was measured following the last growing season in this study, making it unlikely that the population crash had a large effect on our results. We may expect, however, that the trophic effects of GKR on plants will diminish greatly following multiple years of drought, while the ecosystem engineering effects will be less responsive because burrows deteriorate slowly and last beyond the lifetime of the engineer.

Our study shows that animals can alter precipitation legacies by interacting with plants that drive mechanisms of lagged effects, regardless of the type of interaction by which animals affect plants. Though we found evidence for lagged effects mediated by plant litter, additional mechanisms could have been operating as well. In California annual grasslands, high precipitation increases seed production by grasses (St. Clair, Sudderth, Castanha, Torn, & Ackerly, 2009), causing intense seedling competition the following year that

results in greater grass abundance (Larios, Aicher, & Suding, 2013) and lower abundances of other plants (DiVittorio et al., 2007). Kangaroo rats may have also influenced precipitation legacies occurring via seed production and seedbank composition, but this mechanism requires further study. In addition to the above mechanisms, in perennial systems animals may alter precipitation legacies by affecting resource storage in roots, vegetative propagule production, or soil properties influenced by plants that create lag effects. Thus, subterranean herbivores may play a larger role in determining precipitation legacies driven by perennial plants. Irrespective of the type of ecosystem, we anticipate that animals that have large effects on plants will be most likely to modify the strength of precipitation legacies. Dominant herbivores and soil engineers are obvious candidates for such an ecological role, but subdominant herbivores that specialize on plants responsible for lag effects could be important as well. Additionally, animals at higher trophic levels may indirectly influence precipitation legacies, for instance through ecosystem engineering interactions or by generating trophic cascades (Estes et al., 2011; Grinath, Inouye, & Underwood, 2015; Hairston, Smith, & Slobodkin, 1960).

Precipitation legacies continue to be discovered in grasslands and other ecosystems (Anderegg et al., 2015; Dunnett, Willis, Hunt, & Grime, 1998) around the world. These discoveries, as well as those described here regarding animal effects on precipitation legacies, have implications for understanding the stability of plant communities and the ecosystem functions and services that plants support. Temporal variability in plant communities is coming into greater focus as ecologists develop more precise models that include lagged dynamics (Anderegg et al., 2015; Ogle et al., 2015; Wiegand, Snyman, Kellner, & Paruelo, 2004). As future research efforts continue to refine these models, ecologists may need to consider the effects of animals on precipitation legacies to further improve model predictions and guide management efforts.

AUTHORS' CONTRIBUTIONS

All authors contributed to conceiving and designing the methodology. J.W.C., L.R.P. and J.S.B. collected the data; J.B.G. conducted statistical analyses and led writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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