SPECIAL FEATURE ARTICLE

Herbivory enhances the effect of environmental variability on plant community composition and beta diversity

Alejandro Brambila[1] (iD)　|　John W. Chesnut[2]　|　Laura R. Prugh[3]　|　Lauren M. Hallett[1] (iD)

[1]Environmental Studies Program and Department of Biology, University of Oregon, Eugene, OR, USA

[2]Independent Researcher, Los Osos, CA, USA

[3]School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA

Correspondence
Alejandro Brambila, Environmental Studies Program and Department of Biology, University of Oregon, Eugene, OR, USA.
Email: abrambil@uoregon.edu

Abstract

Aim: Understanding the factors that shape biodiversity over space and time is a central question in ecology. Spatiotemporal environmental variation in resource availability can favor different species, generating beta diversity patterns that increase overall diversity. A key question is the degree to which biotic processes—in particular herbivory—enhance or dampen the effect of environmental variation on resource availability at different scales.

Location: We tested this question in a semi-arid California grassland, which is characterized by high rainfall variability. The system supports giant kangaroo rats (*Dipodomys ingens*), which form mounds that structure spatial variability in soil nutrient availability.

Methods: From 2008 to 2017 we implemented a cattle herbivory exclusion experiment to test whether herbivory moderates the effect of spatial and inter-annual resource variability on plant biomass and diversity both on and off mounds.

Results: Grazing reduced local diversity regardless of mound status or amount of precipitation. However, we found that plant productivity was higher on than off mounds, increased following high rainfall years, and that grazing increased these on- versus off-mound differences in wet years—especially after a major drought. Correspondingly, grazing led to on-mound communities that were more different from each other and from off-mound communities.

Conclusions: Taken together, our results suggest that herbivory generally enhances habitat heterogeneity across this arid landscape, but is resource context-dependent with greater effects seen in wetter years.

KEYWORDS
Carrizo Plain, grassland ecology, grazing, resource variability, scales of diversity

1 | INTRODUCTION

Understanding the factors that shape biodiversity over space and time is a central problem in ecology. Bottom-up resource availability and top-down consumer pressure are two key drivers that structure species diversity and interactions (Buckling, Kassen, Bell, & Rainey, 2000; Grime, 1979; Mittelbach et al., 2001; Tilman, 1982) Both drivers are classically associated with a unimodal diversity relationship, such that diversity peaks at intermediate levels of resource availability and consumer pressure. While these processes were initially identified in isolation, more recent theory indicates that they are linked, with herbivory enhancing diversity under high resource conditions and decreasing diversity under low (Borer et al., 2014; Hillebrand et al., 2007; Worm, Lotze, Hillebrand, & Sommer, 2002). However, support for this theory

is mixed, leading to debate around the context (Harrison, Inouye, & Safford, 2003; Mittelbach et al., 2001) and mechanism (Koerner et al., 2018) of resource–consumer–diversity relationships. Potential explanations for this theory focus on the switch from below-ground competition in resource-poor contexts to above-ground competition for light and space in resource-high contexts and the role of dominant versus rare species in each context (Osem, Perevolotsky, & Kigel, 2002). Milchunas, Sala, and Lauenroth (1988) suggest that herbivory and low water resource conditions lead to convergence of plant communities with similar avoidance and tolerance strategies.

Systems with high spatiotemporal variation in resource availability may lead to divergent resource–consumer–diversity relationships within the same site. For example, herbivory may have a differential effect on community dynamics in high versus low resource years and/or patches. Moreover, these dynamics may change with spatial versus temporal resource variation. For example, productivity (Huxman et al., 2004) and species richness (Hawkins et al., 2003; Kreft & Jetz, 2007) are both highly responsive to precipitation across spatial gradients, but their sensitivity to temporal variation in precipitation depends on the environmental context. Specifically, xeric sites exhibit higher sensitivity than mesic sites to intra-annual precipitation variability in both productivity (Huxman et al., 2004) and richness (Adler & Levine, 2007; Cleland, Röder, Azcárate, & Peco, 2013). As such, the positive effect of herbivory on diversity may increase with spatial variation but be overwhelmed by temporal variation in resource availability. Finally, there may be an interaction in which herbivory more strongly moderates diversity in relation to temporal resource variability in high rather than low resource areas.

In systems characterized by high spatiotemporal resource variability, herbivory may alter both local and landscape diversity patterns. Classically, resource–consumer–diversity relationships have focused on patterns in alpha diversity. However, in patchy resource environments, herbivory may also alter landscape patterns of community dissimilarity and dispersion between and within different resource patch types (Anderson et al., 2011; Tuomisto, 2010; Vellend, 2001). Further, these dynamics may only manifest once a baseline level of resources is available. Incorporating data across a range of temporal environmental conditions may more accurately describe communities in variable systems by taking into account changes in species composition across time, whether at the local or landscape level (Avolio et al., 2015). Permanent plots stratified across spatially heterogeneous landscapes and repeatedly sampled across a range of temporal environmental variation can help develop an understanding of a hierarchy of factors structuring plant communities.

The Carrizo Plain, an arid grassland in southern California, is an excellent system to test how herbivory moderates diversity under high spatiotemporal resource variability. First, like many western grasslands, the Carrizo Plain experiences high precipitation variability, and water is a major limitation to plant productivity. Multiple-year droughts are interspersed with wet spells, altering both total plant productivity and functional-group representation (Grinath et al., 2018). Second, the Carrizo Plain is characterized by high spatial resource availability due to the presence of the giant kangaroo rat

(GKR; *Dipodomys ingens*), an ecosystem engineer that forms evenly spaced mounds over six meters in diameter around its burrows (Grinnell, 1932). The mounds increase soil nutrient availability and support more productive plant communities compared to the spaces between mounds, particularly in wet years (Prugh & Brashares, 2012). This spatial resource heterogeneity leads to distinct on-mound plant communities compared to the surrounding inter-mound space (Grinath, Larios, Prugh, Brashares, & Suding, 2019). In addition to ecosystem engineering, the GKR is a major source of herbivory through seed predation (Gurney, Prugh, & Brashares, 2015). Cattle grazing, which is common in the Carrizo Plain and surrounding areas, adds to overall herbivory pressure although GKR regularly consume more biomass than cattle (Endicott, Prugh, & Brashares, nd).

Here we use a long-term (10 years) cattle grazing removal experiment at the Carrizo Plain to assess how cattle grazing (as additional herbivory pressure above baseline GKR herbivory) alters productivity, species diversity and community composition in relation to spatial and temporal resource variability. We hypothesize that given the site's aridity, productivity will increase both on and off mound with inter-annual variation in rainfall, although reduced soil resource availability off mound will limit the increase in productivity off mound leading to increased resource heterogeneity in wet years. Alternatively, the response of productivity to resource conditions could be unimodal, with compensatory growth making up for losses to herbivory in the highest resource conditions. Across variable resource conditions, we expect that grazing will generally reduce productivity, although we expect this effect to vary in its magnitude with minimal effects in low resource conditions, and increasing as there is more total productivity. Because Carrizo Plain is an arid system with generally low average moisture conditions, we expect that diversity will generally increase with precipitation, especially off mound where resource-acquisitive dominants may be limited by existing soil nutrients as well as precipitation. According to the linked resource–herbivory theory, we expect that grazing will reduce diversity under low resource (precipitation and soil nutrient) conditions by increasing mortality but increase diversity in high resource conditions by reducing above-ground competition. Across this heterogeneous landscape, we expect minor effects of grazing on beta diversity in dry years as the whole site is moisture-limited, and a homogenizing effect in wet years as cattle increase diversity on higher resource GKR mounds, but decrease it off mound. Below, we test these patterns both at the local and landscape level and relate them to underlying shifts in species composition and productivity.

2 | METHODS

2.1 | Study area

The Carrizo Plain is the largest remnant of the San Joaquin Valley grassland ecosystem type. The plain is located in the southern part of the valley and is characterized by an arid Mediterranean

climate with mild wet winters and hot dry summers. Average annual precipitation is 190 mm, nearly all of it falling during the growing season which begins in October and ends in April. Annual precipitation is highly variable; during our study, the maximum amount of precipitation fell in 2010–2011 (410 mm), and the minimum in 2013–2014 (46 mm) (1998–2017; MesoWest CAZC1, 35.10° N, 119.77° W). Our study site, Center Well pasture, is located within the Carrizo Plain National Monument. The site has been intermittently grazed by cattle since the 1800s, and it was cultivated for wheat and barley from 1890 till 1974. Contrasted with neighboring pastures that retain a significant native perennial grass cover (i.e. *Poa secunda*), the Center Well plant community within our site is primarily composed of annual forbs (*Erodium cicutarium*, *Lepidium nitidum*) and exotic annual grasses (i.e. *Bromus madritensis*, *Schismus arabicus*, *Hordeum murinum* (species names: Baldwin & Goldman, 2012)). The site is within the endangered GKR's core habitat, whose mounds cover roughly 50% of the soil surface (Gurney et al., 2015). In addition to the GKR there are various rare and endangered endemic plant species concentrated in the Carrizo Plain, of which one, *Monolopia congdonii*, is found in Center Well pasture.

2.2 | Sampling design

Four pairs of 1.96 hectare (140 m × 140 m) control and exclosure plots were randomly placed within the ~5 km × 5 km Center Well pasture. Control plots allowed continued cattle grazing access, and exclosure plots were fenced to eliminate cattle herbivory (but not GKR). Pairs were oriented in a random compass direction and separated by a 60 m buffer. Within each plot, eight 1 m × 1 m quadrats were established to monitor plant communities. These were stratified so that four quadrats were randomly placed on GKR mounds and four were off mounds. Taken together, cattle grazing and GKR mound status comprised our four experimental treatment groups: grazed on-mound, grazed off-mound, ungrazed on-mound, and ungrazed off-mound. Here and throughout, "ungrazed" refers to cattle grazing, and not the presence of GKR or other potential herbivores (i.e. insects). Over time as GKR had continued access to the plots, some mounds shifted and affected quadrats were reclassified, leading the design to become slightly unbalanced by the end of the experiment (Appendix S1). In 2015, new quadrats were established in the cattle exclosure plots, replacing the old plots and rebalancing the on-to-off mound ratio in these plots. Plant communities were assessed at peak productivity (late March to early April) in 1-m^2 quadrats using pin frames. Pins were dropped from above spaced evenly every 10 cm within the quadrat for a total of 81 pin drops. Each first hit was recorded, and one additional hit was recorded for each species that occurred in the quadrat but was not hit. Above-ground net primary productivity (ANPP) was clipped at peak in April, in rotating 1/4 m × 1/4 m plots adjacent to quadrats. This biomass was dried and then weighed for analysis. Cattle grazing occurred in the spring, after

April community and ANPP monitoring. Cattle were only grazed in wet years, specifically 2008–2011 and 2016–2017. To account for legacy effects of grazing we included all years in our analysis based on exclosure status rather than only including data from actively grazed years. We sourced growing-season precipitation data from the University of Utah's MesoWest station CACZ1 (35.10° N, 119.77° W) in the Carrizo Plain.

2.3 | Analysis

2.3.1 | Design/Rainfall

We used R for all statistical analyses (R Core Team, 2017, version 3.4.2). To address temporal variability in water resources, we aggregated rainfall from the summer before to the summer after growth (i.e., previous year July to July) to capture growing-season rainfall (95% of precipitation falls from October to April). We categorized years as wet or dry if they were ±0.5 standard deviation from mean rainfall over the course of the experiment. We considered 2010, 2011 and 2017 as wet years (all grazed) and 2013, 2014 and 2015 as dry years (not grazed). All other years were considered "normal" and excluded from wet or dry categorical analyses as normal year results were intermediate and not significantly different from all year results. Given a major drought that took place during the experiment, we also explicitly analyzed plant communities in 2014, the driest year of the drought, and 2017, the wettest year after the drought to evaluate drought-recovery-specific responses.

2.3.2 | Productivity

To test how grazing and spatiotemporal resource availability altered ANPP, we used a linear mixed-effect model with precipitation (continuous), grazing (grazed or excluded), GKR mound status (on or off mound), and a grazing × mound interaction as fixed effects and year and quadrat nested within plot pair as random effects using the function "lmer" in the R packages "lme4", and "lmerTest" (Bates, Mächler, Bolker, & Walker, 2015; Kuznetsova, Brockhoff, & Christensen, 2017). To test whether the interaction between grazing and mound (each combination of grazing and mound status) was affected by precipitation, we subsequently analyzed ANPP using ANOVA with grazing (grazed or excluded), GKR mound status (on or off mound) and their interaction as fixed effects and year (when more than one year was used in the model) and quadrat nested within plot pair as random effects within just wet years, just dry years, and within 2014 (the strongest drought year) and 2017 (the wettest year post-drought). To address interactive group differences, we used post-hoc Tukey comparisons using the function "glht" in the R package "multcomp" (Hothorn, Bretz, & Westfall, 2008). To estimate *p*-values we used Satterthwaite's approximation of degrees of freedom.

2.3.3 | Diversity

We quantified alpha diversity as Shannon diversity within each replicate quadrat and year using the function "community_diversity" from the R package "codyn" (Hallett et al., 2019). To assess whether the effects of grazing and spatiotemporal resource availability on ANPP affected quadrat-level diversity, we tested precipitation, grazing and mound status on Shannon diversity in parallel models to our ANPP analysis.

To better understand spatial resource and herbivory interactions at the landscape scale, we characterized beta diversity by assessing how grazing treatment, mound status and their interaction led to compositional turnover across the site. We visualized spatial beta diversity using a four-dimensional non-metric multidimensional scaling (NMDS) using the "metaMDS" function in the R package "vegan" (Oksanen et al., 2017). To test for significant differences between treatment communities, we ran perMANOVA using the "adonis" function in the package "vegan". Second, we characterized beta diversity as dispersion within each grazing × mound treatment. This allowed us to test whether grazing homogenized communities within a treatment category and whether this effect varied by spatial resource conditions. We tested for significant differences in community dispersion around centroids for each treatment using the function "betadisper" in the R package "vegan". Parallel to ANPP and alpha diversity analyses, we conducted both beta diversity analyses across all years, and then within wet versus dry years and within 2014 versus 2017. To quantify relative effect sizes of composition and dispersion differences, we used the function "multivariate_difference" in the R package "codyn" (Hallett et al., 2019).

2.3.4 | Composition

Finally, we considered how individual species and groups of species responded to variable resource and herbivory conditions, and how these species drove local and landscape diversity patterns. We aggregated individual species counts into total counts of three plant functional groups—native and introduced grasses and native forbs—within each year and quadrat. For each of these three groups, we tested effects of precipitation, grazing and mound status on their percent cover in models parallel to our ANPP analysis. For native forbs, we related cover to precipitation with a quadratic rather than a linear model based on maximum likelihood best fit. To identify species with particularly strong affinity for a treatment combination we identified indicator species using the function "multipatt" from the R package "indicpecies" (De Cáceres & Legendre, 2009) using the correlation index function corrected for unequal group sizes. We ran this analysis for all years, wet and dry years separately and within 2014 drought and 2017 wet year post-drought. We used a linear mixed-effects model to test the relationship between introduced grasses and ANPP with percent cover of introduced grasses (continuous), grazing (grazed or excluded), GKR mound status (on or off mound) and a grazing × mound interaction as fixed effects and plot pair as a random effect using the function "lme" paralleling our analysis of ANPP.

3 | RESULTS

3.1 | Productivity

Across all years, ANPP was strongly linked to precipitation, increasing 0.81 g/m^2 per mm of rainfall ($F_{1,7.95}$ = 10.29, p = 0.012, Figure 1) and mound status ($F_{1,121.3}$ = 9.79, p = 0.002). In a reduced model with precipitation removed to test for interactive effects of GKR mound and grazing, grazing did not change the mean value of ANPP but increased the heterogeneity of ANPP, significantly elevating ANPP on mounds but reducing it off mounds across years (77.44 g/m^2 difference between on and off mound, p = 0.011). This on-mound effect was approximately twice as high in wet years (167.81 g/m^2 greater on mound compared to off, p = 0.007) and the difference was greatest in the wet year post-drought, 2017 (407.36 g/m^2 greater on mound compared to off, p = 0.001) (Figure 1). Compared to grazed plots, exclosures had more similar (not significantly different) ANPP on and off mound.

3.2 | Diversity

Precipitation was also a major driver of increased quadrat-level Shannon (alpha) diversity ($F_{1,7.9}$ = 8.69, p = 0.018). In our two-way grazing × GKR mound model, alpha diversity was slightly higher in exclosures across all years (exclosure treatment difference = 0.07, $F_{1,65.4}$ = 12.65, p < 0.001). This effect was consistent in dry years, but disappeared in wet years when considered independently (Figure 2). In wet years, however, diversity was significantly ($F_{1,183.1}$ = 4.29, p = 0.039) lower on mound compared to off.

We addressed beta diversity both as between-treatment community differences and within-treatment community dispersions (differences between replicate communities within the same treatment). There were no significant perMANOVA differences between treatment communities except in 2017, when both mound (p = 0.0001) and grazing treatment (p = 0.0001) main effects led to community differentiation (Figure 3). As such, there were minimal treatment differences (see Appendix S2 for effect sizes). However, the sizes of these effects were elevated in wet years, especially the interactive grazing effect off mound. Mirroring significant perMANOVA differences, the effect sizes were more pronounced in 2017, the post-drought wet year. By contrast, dry years had generally intermediate effect sizes. Full community difference results can be seen in Appendix S2.

Beta diversity patterns differed within each treatment group. Grazing led to significantly more dispersed communities across all years (p = 0.015) (Appendix S2). Generally, on-mound grazed communities were the most dispersed. In wet years, dispersion was

FIGURE 1 Above-ground net primary productivity over time and in relation to grazing treatment and mound status (±*SE*, colored lines), and annual precipitation (gray bars)
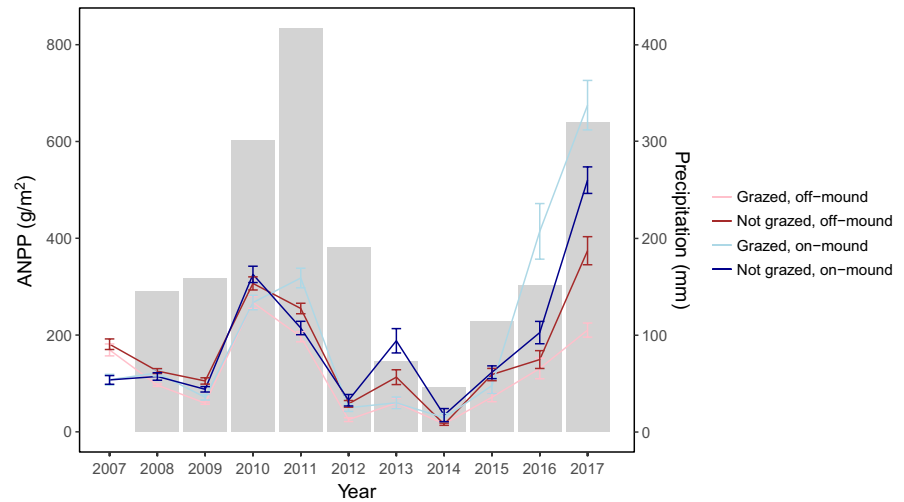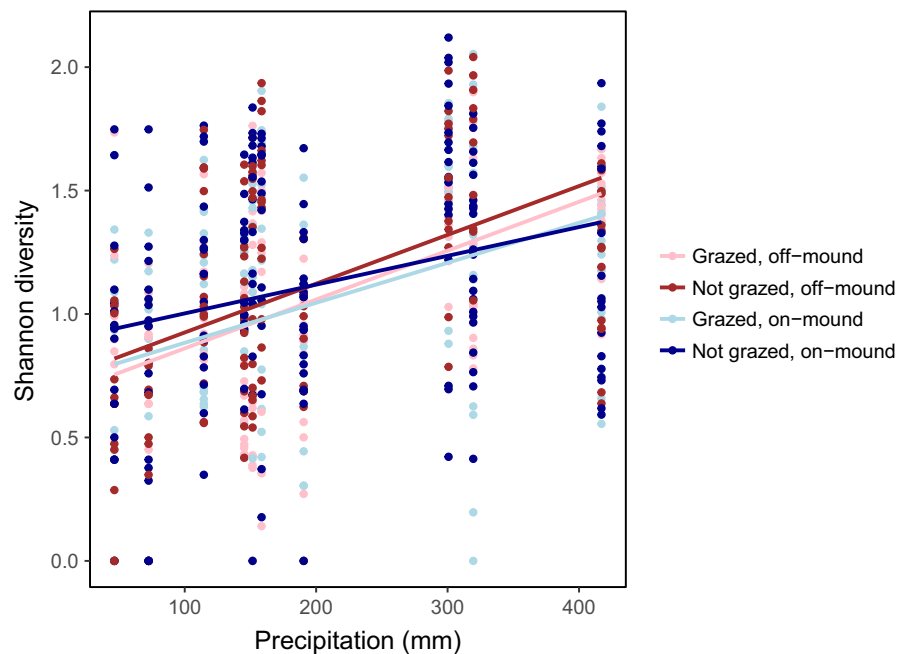

FIGURE 2 Shannon diversity of annual plants in relation to precipitation and grazing treatment and mound status

driven by mound differences and grazing effects were marginal. In the wettest post-drought year, 2017, the effect of grazing was greater compared to wet years generally, increasing dispersion on mound and homogenizing off-mound communities. In dry years (including the driest year, 2014), communities were relatively homogenous, with the exception that on-mound grazed communities had high dispersion (as in all years). Full dispersion results and effect sizes can be found in Appendix S2.

3.3 | Composition

Percent cover of the four introduced annual grass species (Figure 4a) responded positively to precipitation ($F_{1,108.9}$ = 5.69, *p* = 0.018) and there was an interactive effect mirroring the effect on biomass whereby grazing led to a significant difference on and off mound

(difference = 5.5%, *p* = 0.004) across all years, while there was no significant difference between mound status when not grazed. The effect of grazing was consistent in dry years (4.1%, *p* = 0.035) and increased in magnitude in wet years, although it was not significant (7.0%, *p* = 0.076). This effect disappeared in 2014 during the drought (*p* = 0.547), and was largest in 2017 post-drought (21.2%, *p* = 0.003). The three most abundant introduced grasses were *Hordeum murinum*, *Schismus arabicus*, and *Vulpia myuros*. *Schismus* and *Vulpia* cover were not significantly affected by treatment. *Hordeum* emerged as an indicator species for on-mound communities whether grazed or not, and was found on mound with significantly higher cover across all years (9.2%, $F_{1,141.4}$ = 12.53, *p* < 0.001), in wet years (19.72%, $F_{1,47.5}$ = 10.80, *p* = 0.001), and in 2017 (21.05%, $F_{1,42.4}$ = 11.52, *p* = 0.001); but not in dry years or in 2014. Native grasses (mainly one species, *Vulpia microstachys*, which was an indicator species for all but ungrazed on-mound communities) generally increased with
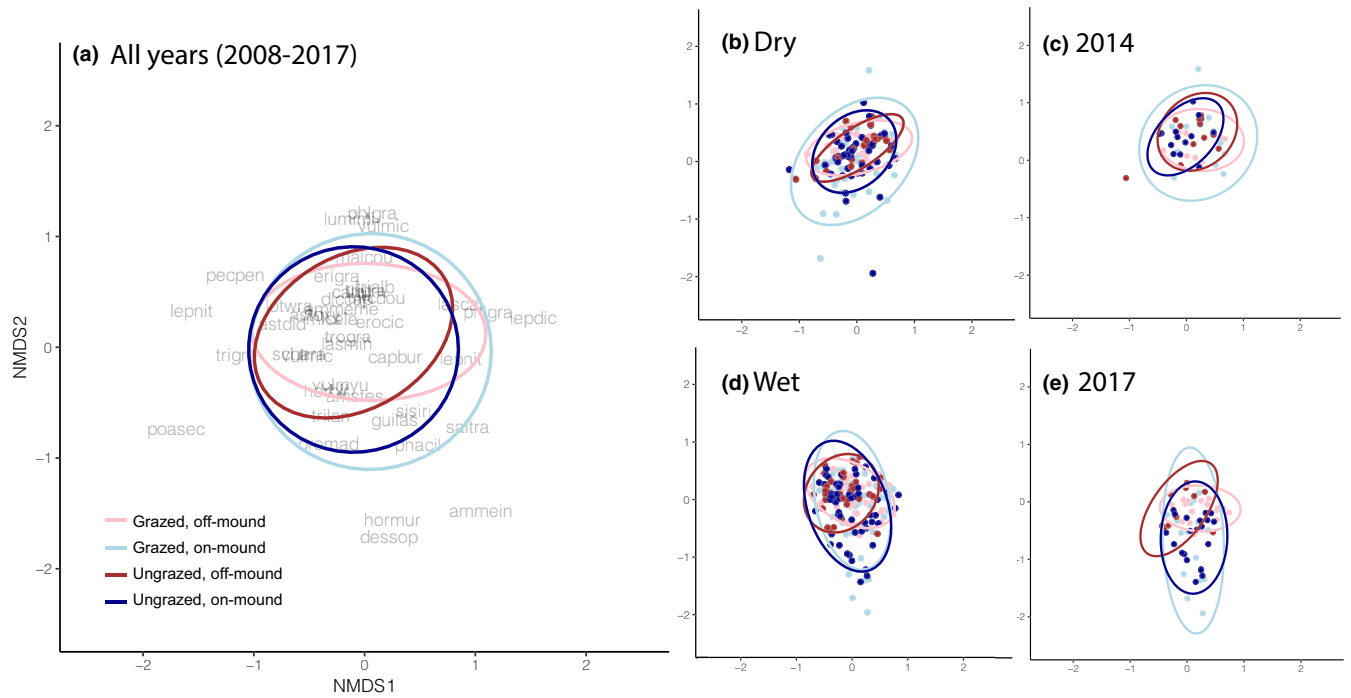
FIGURE 3 NMDS ordinations of communities by treatment in: (a) all years showing ellipses and species positions; (b) dry years; (c) 2014, the driest year over the course of the experiment; (d) wet years; and (e) 2017, the wettest year emerging from the drought. See Appendix S3 for species codes and information
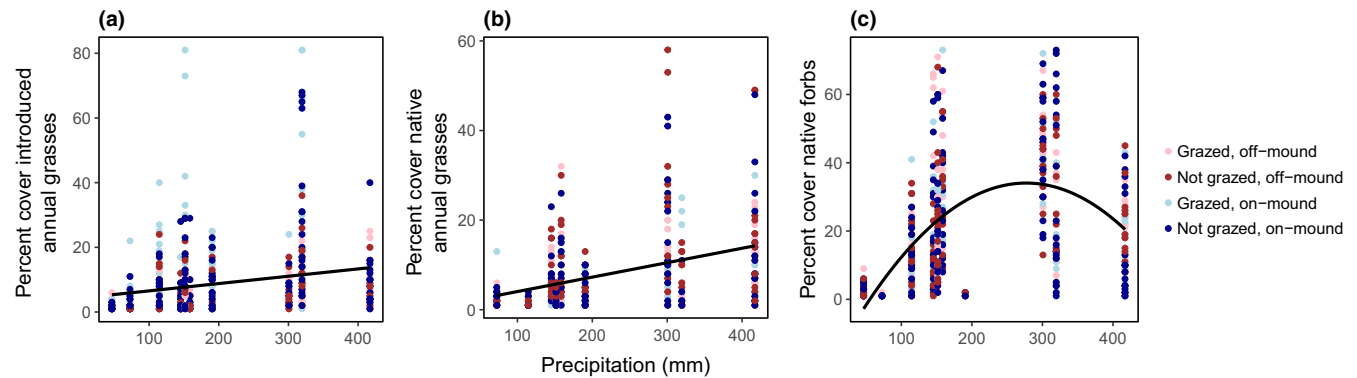

FIGURE 4 Functional-group responses to precipitation and in relation to grazing treatment and mound status

precipitation and were higher on mound, but these results were not significant when random effects of year and location were considered (Figure 4b).

Native forbs, the most species-rich group ($n = 25$), had a unimodal response to precipitation as a continuous variable where their cover peaked at intermediate levels of precipitation, although as with native grasses, this effect was not significant (Figure 4c). As a group, native forb cover did not respond to grazing or mound status. Certain species did, however, have specific responses. The four most common native forbs were all indicator species. *Guillenia lasiophylla* was an indicator of ungrazed, on-mound communities, *Lepidium nitidum* indicated grazed off-mound communities, *Lasthenia minor* indicated ungrazed communities generally, and *Trichostema lanceolatum* indicated ungrazed off-mound communities. The less common *Trifolium gracilentum* and *Microseris elegans*

also emerged as indicators of ungrazed off-mound communities. While some of the more common species responded positively to grazing, less common native forbs, aggregated as "wildflowers", were less abundant on mound than off across all years (1.22% lower, $F_{1,917} = 11.25$, $p < 0.001$), and in dry years responded negatively to grazing off mound (2.60% lower, $F_{1,58} = 11.5$, $p < 0.001$).

Overall, biomass was positively correlated with percent cover of introduced annual grasses across mound and grazing statuses ($F_{1,530} = 56.1$, $p = 2.2e\text{-}13$), although its effect size varied. The effect was approximately five times stronger (coefficient 0.49 vs. 0.11) when grazed versus ungrazed, and while there was a significant relationship on mound, there was no consistent relationship off mound. In summary, biomass was most strongly correlated with introduced grasses in grazed on-mound quadrats, and least correlated in grazed off-mound quadrats.

4 | DISCUSSION

Theoretical (Hillebrand et al., 2007; Milchunas et al., 1988; Proulx & Mazumder, 1998; Proulx, Pick, Mazumder, Hamilton, & Lean, 1996) and empirical developments (Asgari & Steiner, 2017; Groendahl & Fink, 2017; Guerry & Menge, 2017) have led to a general expectation that the effect of herbivory on diversity shifts with resource availability. Here, we tested whether resource–consumer–diversity relationships vary in a highly patterned system with variation in both water resources (temporally) and soil nutrients (spatially). We focused on an arid grassland in which an ecosystem engineer creates high spatial resource variability at a relatively small scale in an otherwise (aspect, slope) homogenous landscape, and in which rainfall is highly variable. Over the course of our study, which included wet periods and a severe, multiyear drought, species diversity and productivity both linearly increased with precipitation. Despite periods and patches of high resource availability, cattle grazing had a small but consistently negative effect on alpha diversity across all years, as theory would predict under consistently low resource conditions (Tilman, 1982). This suggests that average resource conditions in this arid system may be more important than resource variability for local resource–consumer–diversity relationships. However, on high resource patches and especially in wet years, both productivity and beta diversity were enhanced by cattle grazing, in part because grazing was associated with patchy distributions of introduced annual grasses. As such, our findings suggest that resource–consumer–diversity relationships may shift when assessing local versus landscape-level diversity.

Working across a range of spatiotemporal water availability, previous studies have shown that grazing effects do in fact vary within a site (Carmona et al., 2012; Osem et al., 2002; Rota, Manzano, Carmona, Malo, & Peco, 2017). Specifically, these studies find that grazing has the greatest effect on diversity at high resource conditions, although this effect was variable. While Osem (2002) and Carmona (2012) found increases in diversity, Rota (2017) saw a decrease. This is likely due to differences in palatability of dominant and rare species. For example, if the dominant species is a palatable, resource-acquisitive grazing tolerator (as in Carrizo), grazing may increase diversity; but if rare species are more suited to high resource conditions and are not resistant to grazing, grazing may decrease richness. For this reason, it may be important to consider measures of diversity that include evenness.

Productivity and local diversity consistently increased with precipitation, even in the wettest years of this study. This suggests that precipitation was a dominant limiting resource on plant productivity across years, and that peak theoretical diversity likely did not occur across this landscape (Goldberg & Miller, 1990; Grime, 1979; Noy-Meir, 1973). This is consistent with studies that have found evidence for water limitation throughout North American grasslands generally (Sala, Parton, Joyce, & Lauenroth, 1988; Webb, Lauenroth, Szarek, & Kinerson, 1983), and a dominant intra-annual effect of precipitation on both diversity (Cleland et al., 2013) and productivity (Huxman et al., 2004) in arid systems. While a strong effect of

precipitation is not a surprise in our arid system, this effect was consistent regardless of spatial variability or grazing status, suggesting that precipitation is not only a limiting factor, but the major factor structuring plant communities in this system. While soil nutrients did matter (there was greater diversity off mound than on in wet years), their spatial variability may be dampened as nutrient availability can be restricted by moisture limitation (Cardinale, Hillebrand, Harpole, Gross, & Ptacnik, 2009). While these results are consistent with a recent study showing that precipitation plays a substantial role in structuring plant communities in Carrizo, lag effects can lead to unexpected patterns via thatch accumulation in subsequent years (Grinath et al., 2018). In this case, grasses can create a positive feedback where, once established, they increase their dominance over time. Prolonged droughts may function to interrupt and balance this cycle, or as in Sasaki et al. (2009) grazing in wet years can reduce thatch accumulation.

Cattle grazing had a small but significant negative effect on alpha diversity regardless of spatial and temporal resource variability. Given the high degree of spatiotemporal resource variability in the system, it was notable that the consumer effect was stable across conditions. This suggests that, at least in arid systems, resource–consumer–diversity predictions may be most appropriate in relation to average resource conditions, under which herbivory would be expected to further reduce population sizes and increase likelihood of local extinctions (Hillebrand et al., 2007; Worm et al., 2002). In variable but arid systems, periods of high resource conditions may not be enough to shift the community to space and light limitation (Noy-Meir, 1973). As such, there may not be a strong mechanism for grazing to enhance diversity under periodic as opposed to sustained resource availability. This is consistent with results from previous studies on grazing and spatiotemporal resource variability that found greater interactive effects of consumer pressure in relation to spatiotemporal resource variability under slightly higher average resource conditions such as semiarid or mesic grasslands (Carmona, Mason, Azcárate, & Peco, 2015; Carmona et al., 2013; Milchunas et al., 1988). That said, arid systems are often managed for the expectation that grazing has a stronger negative effect under drought conditions, and the Carrizo Plain is no exception. Consequently, it is possible that even greater reductions in local diversity would have occurred if the site were grazed during the drought. While our experimental design is unable to test these effects, it demonstrates that even a carefully managed grazing program can lead to reductions in diversity in arid systems.

Although cattle grazing had a consistent negative effect on local diversity, it enhanced landscape-level beta diversity, especially under high resource conditions. When grazed, on- and off-mound communities diverged, particularly in wet years in an effect that peaked after recovery from the drought in 2017. Focusing exclusively on alpha diversity overlooks these landscape effects, which are driven by community compositional difference on and off mound (Avolio et al., 2015; Stein, Gerstner, & Kreft, 2014). By taking into account between-treatment community distances, we found that grazing increased beta diversity, potentially acting as

a mechanism for increased species coexistence at the landscape scale (Amarasekare, 2003; Chesson, 2000). This community divergence was linked to an increased divergence in productivity in grazed plots in wet years. This result complicates the theoretical resource–consumer–diversity patterns expected whereby consumers affect diversity by reducing productivity (Bartolome, Stroud, & Heady, 1980). Cattle do not consume plants randomly, and through selective feeding they can increase productivity by stimulating the growth or dominance of herbivory-tolerant or less favored species (Koerner et al., 2018). Grazing also can affect plant growth through increasing nutrient cycling by modifying root to shoot ratios, impacting soil texture, and digesting plants into feces (Peco, Navarro, Carmona, Medina, & Marques, 2017) If cattle preferentially spend time on GKR mounds, they may further concentrate nutrients across the landscape, exaggerating the differences in nutrient availability on and off mound. Grazing also increased within-treatment beta diversity (dispersion) particularly in on-mound communities. This again aligns with previous work in variable resource habitats where high resource conditions are more affected by grazing, but in this case the resource in question is soil fertility rather than moisture. While between-treatment beta diversity represents a directional, systematic effect of grazing across the landscape, dispersion represents random patchy effects of grazing. For example, grazing disturbance can create opportunistic habitat for grazing-tolerant species or refuges for rare species (e.g. *Monolopia congdonii)* by creating gaps for colonization and increasing resource turnover (D'Antonio, Dudley, & Mack, 1999).

To understand how scales of diversity interact across our site, we considered species composition. For alpha diversity to stay the same or decrease while beta diversity increases, we expect to see species sorting into landscape patches where they can successfully compete and persist. Specifically, theory predicts that superior competitors for scarce resources will succeed in low resource conditions, and more acquisitive species will better compete for light and space in high resource conditions (Borer et al., 2014; Cardinale et al., 2009; Harpole & Tilman, 2007). The two main types of plants present in our pasture were annual grasses (native and exotic), which both responded positively to increased precipitation, and annual forbs, which represented most of the species diversity and whose percent cover peaked at intermediate precipitation but declined in the wettest years. This unimodal response to increasing resources suggests a transition from abiotic limitation to biotic limitation, and that in high resource contexts grasses tend to outcompete forbs. In fact, introduced annual grass cover drove beta diversity patterns in high resource contexts. Their cover was highest on mound and in wet years, coinciding with highly productive conditions. This result is consistent with observations at Carrizo Plain throughout the 20th century (Grinnell, 1932; Schiffman, 1994) and in western grasslands generally (Huenneke, Hamburg, Koide, Mooney, & Vitousek, 1990; Weiss, 1999). Our indicator species analysis showed that in addition to outcompeting forbs in optimal conditions, these resource-acquisitive exotic grasses (i.e. *Hordeum*) drove the main native grass, *Vulpia microstachys* off mound. While specific native forbs tended to have

more idiosyncratic responses to grazing and mound status, these responses demonstrate filtering by some criteria. Further research is necessary to determine the likely resource and herbivory-resistant trait-mediated responses of individual species. Consistent with previous studies in Carrizo Plain (Kimball & Schiffman, 2003), but contrary to the typical pattern found across California grasslands (Hayes & Holl, 2003; Safford & Harrison, 2001), grazing reduced cover of most forbs (and *Vulpia*), particularly in wet years, potentially because these native species did not evolve with cattle grazing. It is possible that our study differed in this respect due to a first-hit sampling design, which may capture the dynamics of tall grasses but underestimate understorey forbs in years with high grass cover.

In a study of the effects of GKR foraging and mound formation on precipitation legacies, Grinath et al. (2018) also found that GKR mounds led to more introduced annual grasses in wet years. While in our study cattle grazing exaggerated these differences, Grinath et al. (2018) found that GKR foraging effectively suppressed introduced grass cover. These differences may be due to cattle versus GKR feeding preferences, coevolutionary histories with forage species, or direct interactions between cattle and GKR. GKR are substantial grazers in the Carrizo Plain, and regularly remove more ANPP than cattle (Endicott et al., nd). While GKR will selectively forage some species over others, a feeding preference study found they preferred (*Bromus*, *Schismus*) or did not avoid (*Hordeum*) introduced annual grasses (Gurney et al., 2015). As granivores, GKR remove reproductive propagules of plants they consume, while cattle do feed on seeds but prefer leaves over reproductive stems (Reppert, 1960). Cattle organize their foraging activity primarily at the community/patch level, a tendency that is likely exaggerated in Carrizo with cattle spending most of their time on GKR mounds where there can be much higher productivity (Senft et al., 1987). This may help explain the dispersion of on-mound communities, which was driven by a few sites that became highly dominated by *Hordeum*.

In our assessment of the effects of herbivory on plant community dynamics in Carrizo Plain, our results demonstrated that it is important to not only consider general resource availability, but spatial and temporal variability within a site. Across our analyses, the effect of cattle grazing was often subtle and depended on an interaction with spatial and/or temporal resource availability as well as the status of GKR, the other major herbivore in the system. For example, the most dramatic beta diversity and ANPP differences arose in 2017 following the severe drought that drastically reduced GKR populations (Grinath et al., 2018). Results from experimental GKR exclosures support the dominant role of GKR in controlling development of grass dominance in high resource conditions (Prugh & Brashares, 2012). Ultimately, cattle grazing decreased diversity at the alpha level, but increased diversity by increasing patchiness across the landscape, both off mound versus on mound and across mounds themselves. Taking within-site heterogeneity into account allowed for a more nuanced exploration of effects on plant diversity, and considering species-specific responses gave further insight into how plant communities were being affected and leading to divergent productivity and diversity responses. These results show how

grazing exaggerates heterogeneity of plant communities across the landscape at the Carrizo Plain, particularly in high resource years, and provide context for managers of arid landscapes concerned with grass invasion or native plant conservation.

AUTHOR CONTRIBUTIONS

LP and JB developed the research design and implemented the experiment; AB and LH conceived of the research idea; LP and JB collected data; AB performed statistical analyses; AB, with contributions from LH, LP and JC, wrote the paper; all authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Data used for this study are a subset of the Carrizo Plains Ecosystem Project. For complete data, see Appendix S4 in the online supplemental material.

ORCID

Alejandro Brambila https://orcid.org/0000-0002-5885-7045
Lauren M. Hallett https://orcid.org/0000-0002-0718-0257

REFERENCES

Adler, P. B., & Levine, J. M. (2007). Contrasting relationships between precipitation and species richness in space and time. *Oikos*, 116(2), 221–232. https://doi.org/10.1111/j.0030-1299.2007.15327.x

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: A synthesis. *Ecology Letters*, 6(12), 1109–1122. https://doi.org/10.1046/j.1461-0248.2003.00530.x

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., … Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters*, 14(1), 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Asgari, M., & Steiner, C. F. (2017). Interactive effects of productivity and predation on zooplankton diversity. *Oikos*, 126(11), 1617–1624. https://doi.org/10.1111/oik.04099

Avolio, M. L., La Pierre, K. J., Houseman, G. R., Koerner, S. E., Grman, E., Isbell, F., … Wilcox, K. R. (2015). A framework for quantifying the magnitude and variability of community responses to global change drivers. *Ecosphere*, 6(12), art280. https://doi.org/10.1890/ES15-00317.1

Baldwin, B. G., & Goldman, D. H. (2012). *The Jepson manual: Vascular plants of California*. Berkeley, CA: University of California Press.

Bartolome, J. W., Stroud, M. C., & Heady, H. F. (1980). Influence of natural mulch on forage production on differing california annual range sites. *Journal of Range Management*, 33(1), 4. https://doi.org/10.2307/3898219

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., … Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, 508(7497), 517–520. https://doi.org/10.1038/nature13144

Buckling, A., Kassen, R., Bell, G., & Rainey, P. B. (2000). Disturbance and diversity in experimental microcosms. *Nature*, 408(6815), 961–964. https://doi.org/10.1038/35050080

Cardinale, B. J., Hillebrand, H., Harpole, W. S., Gross, K., & Ptacnik, R. (2009). Separating the influence of resource "availability" from resource "imbalance" on productivity-diversity relationships. *Ecology Letters*, 12(6), 475–487. https://doi.org/10.1111/j.1461-0248.2009.01317.x

Carmona, C. P., Azcárate, F. M., de Bello, F., Ollero, H. S., Lepš, J., & Peco, B. (2012). Taxonomical and functional diversity turnover in Mediterranean grasslands: Interactions between grazing, habitat type and rainfall. *Journal of Applied Ecology*, 49(5), 1084–1093. https://doi.org/10.1111/j.1365-2664.2012.02193.x

Carmona, C. P., Mason, N. W. H., Azcárate, F. M., & Peco, B. (2015). Inter-annual fluctuations in rainfall shift the functional structure of Mediterranean grasslands across gradients of productivity and disturbance. *Journal of Vegetation Science*, 26(3), 538–551. https://doi.org/10.1111/jvs.12260

Carmona, C. P., Röder, A., Azcárate, F. M., & Peco, B. (2013). Grazing management or physiography? Factors controlling vegetation recovery in Mediterranean grasslands. *Ecological Modelling*, 251, 73–84. https://doi.org/10.1016/j.ecolmodel.2012.12.005

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Cleland, E. E., Collins, S. L., Dickson, T. L., Farrer, E. C., Gross, K. L., Gherardi, L. A., Suding, K. N. (2013). Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology*, 94(8), 1687–1696. https://doi.org/10.1890/12-1006.1

D'Antonio, C. M., Dudley, T. L., & Mack, M. (1999). Disturbance and biological invasions: Direct effects and feedbacks. In: Walker, L. E. (Ed.), *Ecosystems of Disturbed Ground* (Vol. 16). Amsterdam, The Netherlands: Elsevier.

De Caceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*. 90(12), 3566–3574. https://doi.org/10.1890/08-1823.1

Endicott, R., Prugh, L., & Brashares, J. (2016). Carrizo plain ecosystem project annual report. Prepared for the Unites States Bureau of Land Management.

Goldberg, D. E., & Miller, T. E. (1990). Effects of different resource additions on species diversity in an annual plant community. *Ecology*, 71, 213–225. https://doi.org/10.2307/1940261

Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*, 222 pp. Chichester: Wiley. https://doi.org/10.1016/S1540-7489(02)80243-7

Grinath, J. B., Deguines, N., Chesnut, J. W., Prugh, L. R., Brashares, J. S., & Suding, K. N. (2018). Animals alter precipitation legacies: Trophic and ecosystem engineering effects on plant community temporal dynamics. *Journal of Ecology*, 106(4), 1454–1469. https://doi.org/10.1111/1365-2745.12936

Grinath, J. B., Larios, L., Prugh, L. R., Brashares, J. S., & Suding, K. N. (2019). Environmental gradients determine the potential for ecosystem engineering effects. *Oikos*, 128(7), 994–1004. https://doi.org/10.1111/oik.05768

Grinnell, J. (1932). Habitat Relations of the Giant Kangaroo Rat. *Journal of Mammalogy*, 13(4), 305. https://doi.org/10.2307/1374134

Groendahl, S., & Fink, P. (2017). Consumer species richness and nutrients interact in determining producer diversity. *Scientific Reports*, 7(1), 1–8. https://doi.org/10.1038/srep44869

Guerry, A. D., & Menge, B. A. (2017). Grazer impacts on algal community structure vary with the coastal upwelling regime. *Journal of Experimental Marine Biology and Ecology*, 488, 10–23. https://doi.org/10.1016/j.jembe.2016.12.011

Gurney, C. M., Prugh, L. R., & Brashares, J. S. (2015). Restoration of native plants is reduced by rodent-caused soil disturbance and seed removal. *Rangeland Ecology and Management*, 68(4), 359–366. https://doi.org/10.1016/j.rama.2015.05.001

Hallett, L., Avolio, M. L., Carroll, I. T., Jones, S. K., Macdonald, A. A. M., Flynn, D. F. B., … Jones, M. B. (2019). *codyn: Community Dynamics Metrics*. https://doi.org/10.5063/F1N877Z6

Harpole, W. S., & Tilman, D. (2007). Grassland species loss resulting from reduced niche dimension. *Nature*, 446(7137), 791–793. https://doi.org/10.1038/nature05684

Harrison, S., Inouye, B. D., & Safford, H. D. (2003). Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology*, 17(3), 837–845. https://doi.org/10.1046/j.1523-1739.2003.01633.x

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J. F., Kaufman, D. M., … Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84(12), 3105–3117. https://doi.org/10.1890/03-8006

Hayes, G. F., & Holl, K. D. (2003). Site-specific responses of native and exotic species to disturbances in a mesic grassland community. *Applied Vegetation Science*, 6(2), 235–244. https://doi.org/10.1111/j.1654-109X.2003.tb00584.x

Hillebrand, H., Gruner, D. S., Borer, E. T., Bracken, M. E. S., Cleland, E. E., Elser, J. J., … Smith, J. E. (2007). Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences*, 104(26), 10904–10909. https://doi.org/10.1073/pnas.0701918104

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, 50(3), 346–363. https://doi.org/10.1002/bimj.200810425

Huenneke, L. F., Hamburg, S. P., Koide, R., Mooney, H. A., & Vitousek, P. M. (1990). Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology*, 71(2), 478–491. https://doi.org/10.2307/1940302

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., … Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, 429(6992), 651–654. https://doi.org/10.1038/nature02561

Kimball, S., & Schiffman, P. M. (2003). Differing Effects of Cattle Grazing on Native and Alien Plants. *Conservation Biology*, 17(6), 1681–1693. https://doi.org/10.1111/j.1523-1739.2003.00205.x

Koerner, S. E., Smith, M. D., Burkepile, D. E., Hanan, N. P., Avolio, M. L., Collins, S. L., … Zelikova, T. J. (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology and Evolution*, 2(12), 1925–1932. https://doi.org/10.1038/s41559-018-0696-y

Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences*, 104(14), 5925–5930. https://doi.org/10.1073/pnas.0608361104

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26. https://doi.org/10.18637/jss.v082.i13

Milchunas, D. G., Sala, O. E., & Lauenroth, W. K. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, 132(1), 87–106. https://doi.org/10.1086/284839

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., … Gough, L. (2001). What is the observed relationship between species richness and productivity? *Ecology*, 82(9). https://doi.org/10.1890/0012-9658(2001)082[2381:WITORB]2.0.CO;2

Noy-Meir, I. (2003). Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics*, 4(1), 25–51. https://doi.org/10.1146/annurev.es.04.110173.000325

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P., O'Hara, B., … Wagner, H. (2017). Vegan: Community Ecology Package. R Package Version 2.2-1. 2.1-2.

Osem, Y., Perevolotsky, A., & Kigel, J. (2002). Grazing effect on diversity of annual plant communities in a semi-arid rangeland: Interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology*, 90(6), 936–946. https://doi.org/10.1046/j.1365-2745.2002.00730.x

Peco, B., Navarro, E., Carmona, C. P., Medina, N. G., & Marques, M. J. (2017). Effects of grazing abandonment on soil multifunctionality: The role of plant functional traits. *Agriculture, Ecosystems and Environment*, 249, 215–225. https://doi.org/10.1016/j.agee.2017.08.013

Proulx, M., & Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology*, 79, 2581–2592.

Proulx, M., Pick, F. R., Mazumder, A., Hamilton, P. B., & Lean, D. R. S. (2006). Experimental evidence for interactive impacts of human activities on lake algal species richness. *Oikos*, 76(1), 191. https://doi.org/10.2307/3545761

Prugh, L. R., & Brashares, J. S. (2012). Partitioning the effects of an ecosystem engineer: Kangaroo rats control community structure via multiple pathways. *Journal of Animal Ecology*, 81(3), 667–678. https://doi.org/10.1111/j.1365-2656.2011.01930.x

R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Reppert, J. N. (2007). Forage preference and grazing habits of cattle at the eastern Colorado range station. *Journal of Range Management*, 13(2), 58. https://doi.org/10.2307/3895123

Rota, C., Manzano, P., Carmona, C. P., Malo, J. E., & Peco, B. (2017). Plant community assembly in Mediterranean grasslands: Understanding the interplay between grazing and spatio-temporal water availability. *Journal of Vegetation Science*, 28(1), 149–159. https://doi.org/10.1111/jvs.12470

Safford, H. D., & Harrison, S. P. (2001). Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. *Ecological Applications*, 11, 1112–1122.

Sala, O. E., Parton, W. J., Joyce, L. A., & Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. *Ecology*, 69(1), 40–45. https://doi.org/10.2307/1943158

Sasaki, T., Okayasu, T., Ohkuro, T., Shirato, Y., Jamsran, U., & Takeuchi, K. (2009). Rainfall variability may modify the effects of long-term exclosure on vegetation in Mandalgobi, Mongolia. *Journal of Arid Environments*, 73(10), 949–954. https://doi.org/10.1016/j.jaridenv.2009.04.008

Schiffman, P. M. (1994). Promotion of exotic weed establishment by endangered giant kangaroo rats (Dipodomys ingens) in a California grassland. *Biodiversity and Conservation*, 3(6), 524–537. https://doi.org/10.1007/BF00115158

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., & Swift, D. M. (1987). Large Herbivore Foraging and Ecological Hierarchies. *BioScience*, 37(11), 789–799. https://doi.org/10.2307/1310545

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7), 866–880. https://doi.org/10.1111/ele.12277

Tilman, D. (1982). Resource competition and community structure. *Monographs in Population Biology*, 17, 1–296.

Tuomisto, H. (2010). A diversity of beta diversities: Straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography*, 33(1), 23–45. https://doi.org/10.1111/j.1600-0587.2009.06148.x

Vellend, M. (2001). Do commonly used indices of β-diversity measure species turnover? *Journal of Vegetation Science*, 12(4), 545–552. https://doi.org/10.2307/3237006

Webb, W. L., Lauenroth, W. K., Szarek, S. R., & Kinerson, R. S. (1983). Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States. *Ecology*, *64*(1), 134–151. https://doi.org/10.2307/1937336

Weiss, S. B. (1999). Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology*, *13*(6), 1476–1486. https://doi.org/10.1046/j.1523-1739.1999.98468.x

Worm, B., Lotze, H. K., Hillebrand, H., & Sommer, U. (2002). Consumer versus resource control of species diversity and ecosystem functioning. *Nature*, *417*(6891), 848–851. https://doi.org/10.1038/nature00830

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Quadrat classification over time by block

Appendix S2. Beta diversity statistics for main and interactive effects in all years, wet years, dry years, 2014 and 2017

Appendix S3. Table of species sampled in experimental plots. Nomenclature follows Baldwin and Goldman (2012)

Appendix S4. Full cleaned data set used for study; carrizo_cattle.csv