

ARTICLE

Effects of multiple mammalian herbivores and climate on grassland–shrubland transitions in the Chihuahuan Desert

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Abstract

The replacement of grasses by shrubs or bare ground (xerification) is a primary form of landscape change in drylands globally with consequences for ecosystem services. The potential for wild herbivores to trigger or reinforce shrubland states may be underappreciated, however, and comparative analyses across herbivore taxa are sparse. We sought to clarify the relative effects of domestic cattle, native rodents, native lagomorphs, and exotic African oryx (*Oryx gazella*) on a Chihuahuan Desert grassland undergoing shrub encroachment. We then asked whether drought periods, wet season precipitation, or interspecific grass–shrub competition modified herbivore effects to alter plant cover, species diversity, or community composition. We established a long-term experiment with hierarchical herbivore exclusion treatments and surveyed plant foliar cover over 25 years. Cover of honey mesquite (*Prosopis glandulosa*) proliferated, responding primarily to climate, and was unaffected by herbivore treatments. Surprisingly, cattle and African oryx exclusion had only marginal effects on perennial grass cover at their current densities. Native lagomorphs interacted with climate to limit perennial grass cover during wet periods. Native rodents strongly decreased plant diversity, decreased evenness, and altered community composition. Overall, we found no evidence of mammalian herbivores facilitating or inhibiting shrub encroachment, but native small mammals interacting with climate drove dynamics of herbaceous plant communities. Ongoing monitoring will determine whether increased perennial grass cover from exclusion of native lagomorphs and rodents slows the transition to a dense shrubland.

KEYWORDS

African oryx, *Bouteloua eriopoda*, cattle, desert rodents, dryland ecology, grasslands, herbivory, lagomorphs, landscape change, *Prosopis glandulosa*

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INTRODUCTION

Drylands cover 41% of the Earth's terrestrial surface (MEA, 2005) and are particularly vulnerable to transformations triggered by climate because their productivity is limited by precipitation, and drought severity and duration are expected to increase in drylands (Berdugo et al., 2020; Huang et al., 2017). Droughts interacting with livestock overgrazing have already catalyzed landscape change across many drylands (Gaitán et al., 2018; Maestre et al., 2022; Souther et al., 2020). Shrub encroachment into grasslands with expansion of bare ground (i.e., xerification) is a dominant form of landscape change in these drylands (Berdugo et al., 2022; Ding & Eldridge, 2023; Schreiner-McGraw et al., 2020), with subsequent declines in grassland ecosystem services including forage production, soil stabilization, and water flow regulation (Maestre et al., 2022).

Although livestock grazing–climate interactions have been considered key triggers of grassland loss and shrub encroachment, selective herbivory by a suite of large and small mammals may also modulate grassland–shrubland transitions (Davidson et al., 2010). However, the effects of domestic livestock versus wild herbivores on desert ecosystems remain uncertain because studies typically focus on these taxa in isolation (Davies et al., 2023; Maestre et al., 2022). Herbivores also can promote landscape change by altering soil deposition and compaction plus rates of carbon, nitrogen, and hydrologic cycling through trampling, wallowing, burrowing, and defecation (Forbes et al., 2019; Pringle et al., 2023; Tuomi et al., 2019). Detecting such effects of herbivores on vegetation change requires long-term studies because herbivore–climate interactions can play out over decades (Curtin et al., 1999).

In the Chihuahuan Desert, episodes of historical cattle overgrazing interacted with drought to trigger the conversion of vast landscapes dominated by black grama (*Bouteloua eriopoda*) and other grasses to honey mesquite (*Prosopis glandulosa*) shrublands (D'Odorico et al., 2011; Peters et al., 2012). Increasing climate variability (Gherardi & Sala, 2015) and positive feedbacks from reduced fire frequency, shrub-on-grass competition, and soil erosion can reinforce shrub expansion at the expense of grasses (D'Odorico et al., 2011; Pierce, Archer, Bestelmeyer, & James, 2019).

Native rodents and lagomorphs also have been implicated in reinforcing shrubland states, but the role of native herbivores in controlling vegetation change has been equivocal. Among rodents, kangaroo rats (*Dipodomys* spp.) are considered a keystone guild that can reinforce shrub-encroached grasslands through granivory, including selective predation of large-seeded species (Brown & Heske, 1990; Maron et al., 2021), graminivory

(Kerley et al., 1997; Kerley & Whitford, 2009), and soil disturbance from burrowing behavior (Brown & Heske, 1990). Consumption of grass seedlings and herbaceous vegetation by native lagomorphs may also be a causal pathway reinforcing shrub-dominated states (Abercrombie et al., 2019; Bestelmeyer et al., 2007). However, parallel research in the Chihuahuan Desert has shown that rodents and lagomorphs can have little to no effect on grass recruitment and recovery (Báez et al., 2006; Havstad et al., 1999; Svejcar et al., 2019). Low abundances of rodents due to bottom-up regulation from low net primary productivity may explain the absence of rodent effects on vegetation dynamics in some studies (Báez et al., 2006). Outcomes of herbivory studies of native mammals may thus be context dependent, being influenced strongly by how climate affects consumer dynamics (Schooley et al., 2018; Thibault et al., 2010; Wagnon, 2023).

Unmanaged, invasive ungulates also have promoted landscape change globally with negative impacts on biodiversity, soil erosion, and economic viability of local agriculture (Côté et al., 2004; Mihailou & Massaro, 2021; Spear & Chown, 2009), and their effects are more severe in drylands (Augustine & McNaughton, 2006). The African oryx (*Oryx gazella*), or gemsbok, is a large (≥ 200 kg), generalist ungulate species native to the Kalahari Desert with introduced populations increasing in the northern Chihuahuan Desert (Bender et al., 2019). Oryx may exacerbate landscape change there because they prefer grassland habitats, most notably during dry periods (Andreoni et al., 2021), and grasses constitute $\geq 50\%$ of their diet in their exotic range (Cain et al., 2017; Marquez & Boecklen, 2010; Smith et al., 1998). However, the effects of African oryx on imperiled black grama grasslands have yet to be directly assessed.

Here, we hierarchically excluded domestic cattle and exotic oryx, native lagomorphs, and native rodents from a Chihuahuan Desert grassland and evaluated the effects of herbivore–climate interactions on vegetation as this grassland transitioned toward a shrubland over 25 years. We asked whether the effects of experimental manipulations to herbivore access were modified by long-term aridity trends (Christensen et al., 2023), current and legacy precipitation (Goheen et al., 2013; Monger et al., 2015; Sala et al., 2012), and interspecific grass–shrub competition (Pierce, Archer, & Bestelmeyer, 2019; Pierce, Archer, Bestelmeyer, & James, 2019).

Specifically, we tested a set of hypotheses about how climate and herbivores could play crucial and distinct roles in governing grassland–shrubland transitions (Figure 1). During dry periods, we expected shrubs to be favored over grasses due to superior belowground competition for soil water (Pierce, Archer, Bestelmeyer, & James, 2019). If dry periods occurred during early stages of shrub encroachment,

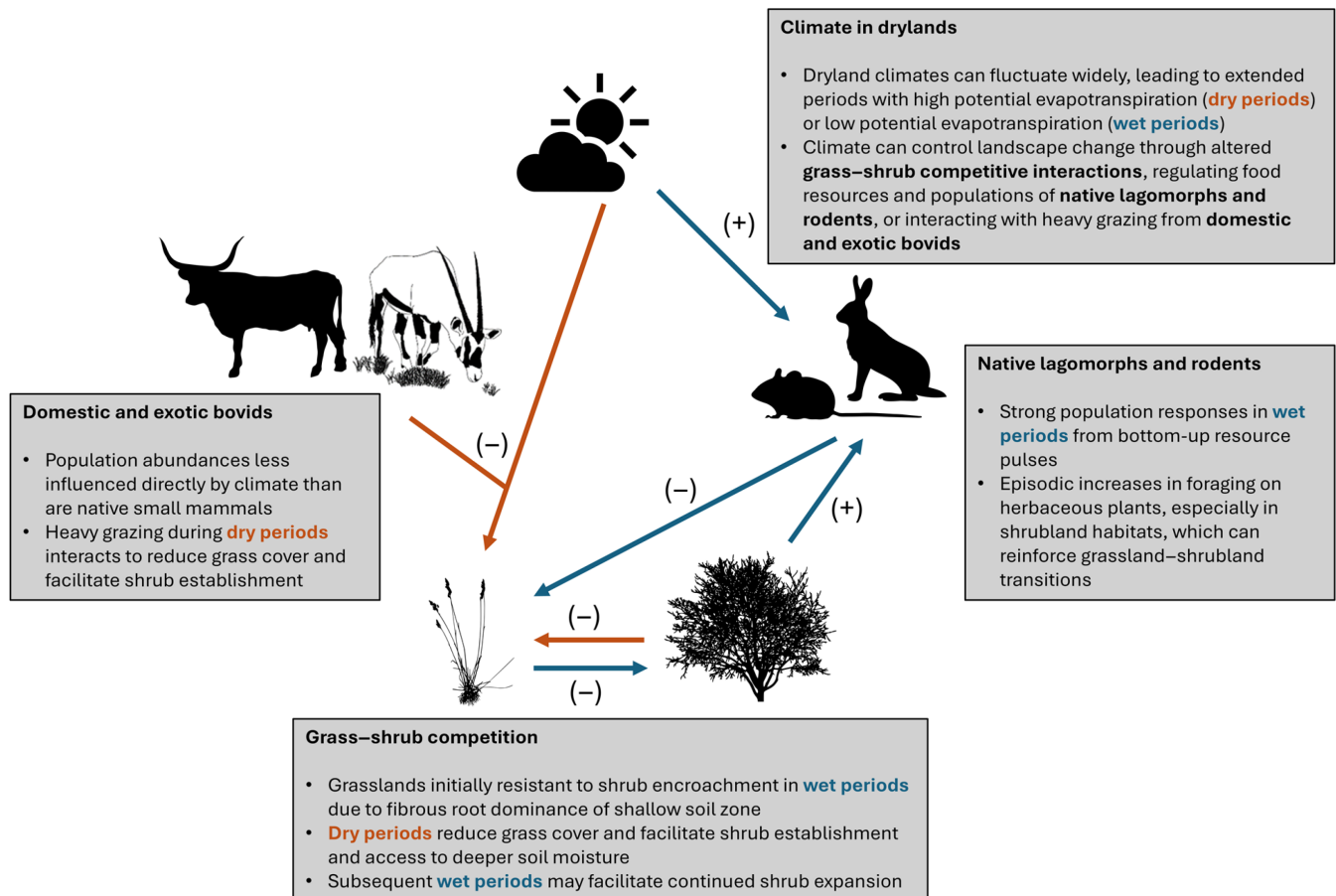


FIGURE 1 Hypothesized relationships among climate, multiple herbivore taxa, and interspecific grass–shrub competition, and how such relationships could contribute to grassland–shrubland transitions in the Chihuahuan Desert. Image credits: oryx, Kieran Andreoni; sun and cloud from Microsoft 365 stock images; all other images (cow, rodent, lagomorph, grass, and shrub) are from PhyloPic under a CC0 1.0 Universal Public Domain Dedication license.

then shrubs would experience competitive release from perennial grasses, advancing the transition toward a shrubland (Pierce, Archer, & Bestelmeyer, 2019). Moreover, we hypothesized that large bovids (cattle and oryx) would interact with drought to further reduce perennial grasses and promote subsequent shrub expansion (D’Odorico et al., 2011). We expected native mammalian herbivores to have relatively weak effects on vegetation during dry periods because their population abundances would be low due to bottom-up regulation (Báez et al., 2006). During wet periods, we hypothesized that perennial grasses would respond positively to both wet season precipitation (Christensen et al., 2023) and previous-year wet season precipitation (i.e., legacy effects; Sala et al., 2012). However, we predicted that native rodents and lagomorphs would reduce herbaceous cover (Bestelmeyer et al., 2007; Brown & Heske, 1990; Kerley & Whitford, 2009) during wet periods when their abundances were high enough to exert top-down control (Schooley et al., 2018; Wagnon, 2023). Finally, we expected desert rodents to drive diversity

and composition of plant communities through selective herbivory (Brown & Heske, 1990; Maron et al., 2021).

METHODS

Study area and herbivore community

The Jornada Basin Long Term Ecological Research (JRN LTER) site is located approximately 35 km north of Las Cruces, New Mexico, USA (32°35′ N, 106°51′ W; 1334 m above sea level). The 100,000-ha site consists of grassland and shrubland communities common to the northern Chihuahuan Desert (Peters et al., 2012). Plant communities relevant to our investigation include black grama grasslands transitioning to honey mesquite shrublands, both occurring within the basin on sandy-to-sandy-loam soils. Other plant species of these grasslands include mesa dropseed (*Sporobolus flexuosus*), spike dropseed (*Sporobolus contractus*), purple threeawn

(*Aristida purpurea*), soaptree yucca (*Yucca elata*), broom snakeweed (*Gutierrezia sarothrae*), longleaf jointfir (*Ephedra trifurca*), and a diversity of annual and perennial forbs (Peters & Gibbens, 2006). Of the annual rainfall at the JRN LTER site (mean = 23 cm, range = 10–40 cm), most occurs during the monsoon season from July to September (mean = 18 cm, range = 7–27 cm) and is driven by the El Niño–Southern Oscillation (Peters et al., 2012).

Mammalian herbivores included four groups: native rodents, native lagomorphs, domestic cattle, and exotic African oryx. The desert rodent community (Lightfoot et al., 2012; Schooley et al., 2018) includes granivorous kangaroo rats (*Dipodomys spectabilis*, *Dipodomys merriami*, *Didodomys ordii*) and pocket mice (*Perognathus flavus*, *Chaetodipus eremicus*), folivorous woodrats (*Neotoma leucodon*, *Neotoma micropus*) and cotton rats (*Sigmodon hispidus*), and omnivorous mice (e.g., *Onychomys* spp.). Collectively, this rodent community irrupted periodically during the study (Appendix S1: Figure S1a) and responds most strongly to resource pulses in shrubland habitats (Schooley et al., 2018). Native lagomorphs include black-tailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) that both feed on perennial grasses and, to a lesser extent, honey mesquite shrubs (Peters & Gibbens, 2006). Lagomorph dynamics were less volatile than for rodents with two peaks in abundance during our study (Appendix S1: Figure S1b). Angus–Hereford cross, Brangus, and Criollo are the prevalent cattle breeds at the JRN LTER site because of their tolerance to extremes of heat and sunlight. Annual stocking rates for cattle were drastically reduced during the 20th century with most pastures receiving light-to-moderate grazing since the start of our experiment (Havstad & Bestelmeyer, 2019). Cattle were removed from the pasture containing our study site in 2008, but oryx relative abundances estimated from camera traps have increased threefold across the JRN LTER site from 0.984 (independent detections per 100 trap-nights) in 2014 to 3.183 in 2018 (Andreoni et al., 2021). Thus, cattle were the dominant bovid during the first portion of our study (1995–2008), and oryx became the dominant bovid during the second portion (2009–2020).

Experimental design

The herbivore exclosure experiment was established in 1995 in a black grama grassland (Lightfoot & Bestelmeyer, 2022). The grassland site (1 × 0.5 km) consisted of four replicate spatial blocks that each included four 36 × 36-m plots ($n = 16$ plots total). Blocks were separated by ~150 m, and

plots within blocks were separated from neighboring plots by ~20 m (Figure 2a). We used a randomized complete block design in which each block included plots receiving three herbivore exclosure treatments and an unfenced control. Unfenced control plots included no manipulations to herbivore access and thus represented background conditions. Treatments excluded only bovids (cattle and oryx) via barbed wire (“-B” treatment), bovids and lagomorphs via barbed wire overlaid by 2.5 × 2.5-cm poultry wire (“-BL” treatment), or all mammal herbivores, including rodents, via barbed wire overlaid by 1 × 1-cm hardware cloth (“-BLR” treatment). Hardware cloth was buried 20 cm in the soil to deter rodent burrowing and affixed at the top with metal flashing to deter rodent climbing (Figure 2b). Exclosure treatments were checked periodically for signs of damage or access by mammals. In particular, if occasional rodent activity was detected within -BLR plots, we removed individuals via livetrapping.

Vegetation cover and precipitation

We measured percent foliar cover and height by plant functional type (i.e., perennial grasses, annual grasses, forbs, shrubs, sub-shrubs), and further by plant species, annually from 1995 to 2005 typically in September–October (Lightfoot & Bestelmeyer, 2022). From 2005 to 2020, sampling frequency was relaxed to every 5 years. Measurements during fall were most relevant to our questions as they represent peak plant biomass for the year following monsoonal rains.

Each plot (treatments and controls) contained thirty-six 1 × 1-m permanent vegetation cover quadrats, spaced 5.8 m from neighboring quadrats. We used these quadrats to estimate mean percent foliar cover for each plant functional type and species for each plot. We focused functional type analyses on the responses of perennial grasses and honey mesquite shrubs because the dominance by either was indicative of whether the ecosystem was in a grassland (high perennial grass cover, low mesquite cover) or shrubland (low perennial grass cover, high mesquite cover) state. We considered honey mesquite as a functional type because it was the main invading shrub species. By 2020, honey mesquite represented 100% of the overall shrub cover on the study site.

We anticipated precipitation could differentially affect perennial grasses and honey mesquite, so we assessed multiple precipitation measures as predictors that represented different temporal scales: annual, wet season, previous wet season (1-year lag), and a 5-year drought index. We used a meteorological station located 1.2 km east-southeast of the study site (Anderson, 2022a; Thatcher & Bestelmeyer, 2023) to measure annual

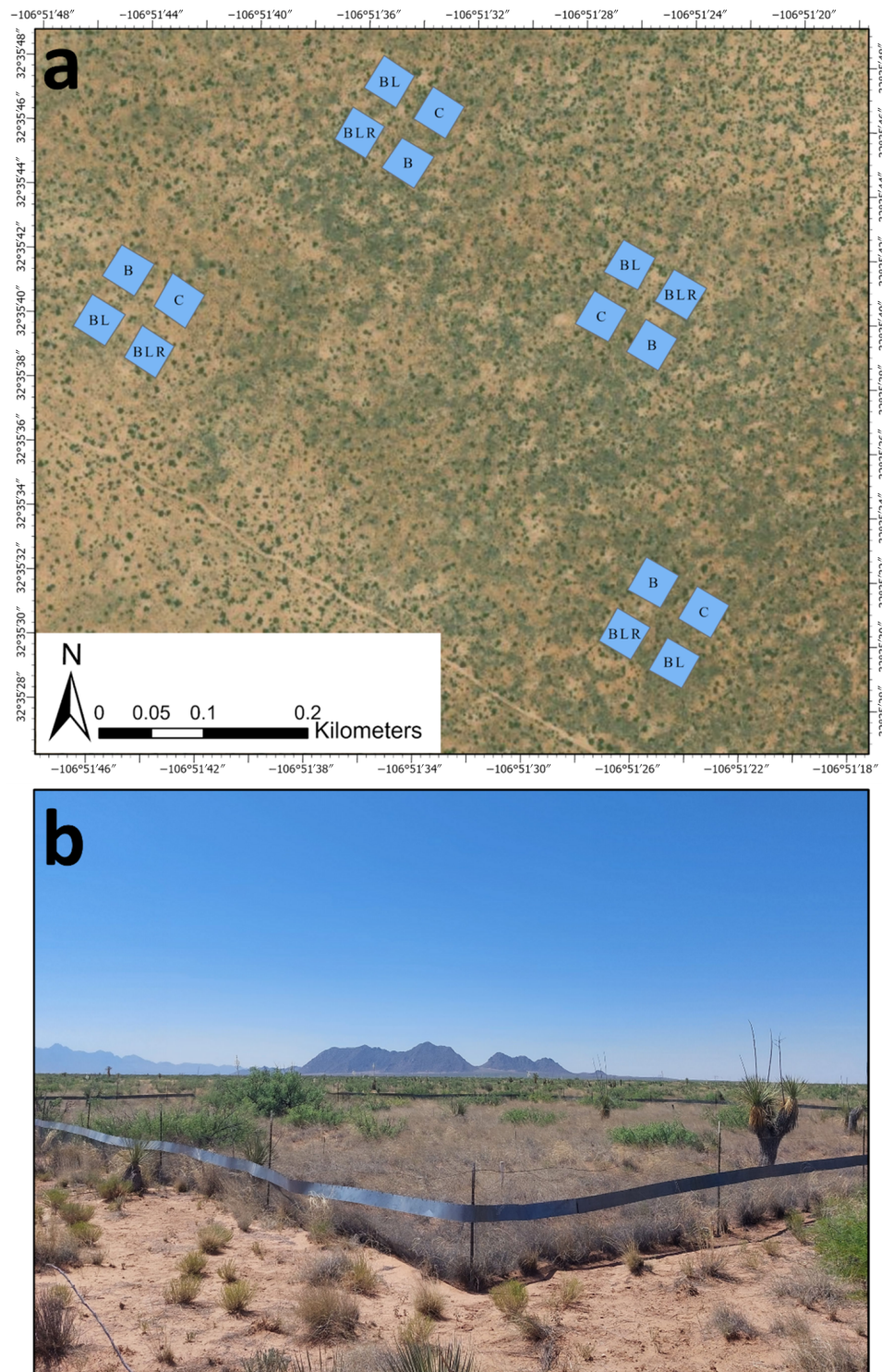


FIGURE 2 (a) Aerial view of the herbivore exclusion experiment at the Jornada Basin Long Term Ecological Research site, New Mexico, USA. Squares represent plots receiving one of three treatments (-B, bovids excluded; -BL, bovids and lagomorphs excluded; -BLR, bovids, lagomorphs, and rodents excluded) or serving as a control. (b) An example of a 36×36 -m plot that excluded all mammal groups (-BLR treatment). The photograph is from July 2023 and shows the surrounding area in foreground with open access to all mammalian herbivores (credit: Kieran Andreoni).

precipitation (October [previous year] – September [current year]) and wet season precipitation (June–September). We calculated the 5-year drought

index using the Standardized Precipitation-Evapotranspiration Index (SPEI) using package “SPEI” (Ver. 1.7; Beguería &

Vicente-Serrano, 2017) in R (Ver. 4.1.3; R Core Team, 2022). The SPEI employs mean monthly air temperature and geographic latitude to calculate potential evapotranspiration (PET). We used a nearby weather station (8.8 km from the meteorological station) to attain mean monthly air temperature (Anderson, 2022b). A monthly water balance is then calculated whereby

$$D_i = P_i - \text{PET}_i; \quad (1)$$

the difference between precipitation P and PET in month i yields a measure of water surplus or deficit D (Vicente-Serrano et al., 2010). Monthly D values were then summed over 5-year periods. Thus, the SPEI values used in analyses were aggregated monthly water deficits and surpluses from the 60 months preceding vegetation sampling. Negative SPEI values indicate water deficits, and positive SPEI values indicate water surpluses.

Statistical analysis

Perennial grasses and honey mesquite

To test our hypotheses, we separately evaluated responses for percent foliar cover of perennial grasses and honey mesquite with linear mixed models in R using package “nlme” (Ver. 3.1-155; Pinheiro et al., 2022). We first incorporated necessary model parameters and structures to satisfy assumptions of normality and residual homogeneity (Zuur et al., 2009). To address dependency among observations within a spatial block, and within herbivore treatment and control plots, we included a random intercept of plot nested within spatial block. Further, because of residual heterogeneity in our null model for perennial grasses, we incorporated an identity variance structure per time stratum, whereby

$$\varepsilon_t \sim N(0, \sigma_t^2), t = 1, \dots, 26. \quad (2)$$

The model residual ε at time step t is normally distributed with a mean of 0 and variance σ^2 that is allowed to vary per time step t . Because we collected repeat measurements of foliar cover in quadrats, we included a continuous, first-order autocorrelation function in our perennial grass models taking the form of

$$h(s, \phi) = \phi s, s \geq 0, \phi \geq 0, \quad (3)$$

such that parameter s accounts for the separation in time between observations and ϕ is the estimated

autocorrelation parameter (Pinheiro & Bates, 2000). We opted for a continuous-time autocorrelation structure because sampling of foliar cover shifted in 2005 from annual to every 5 years, creating unequal time steps. We used a first-order compound symmetry autoregressive structure for all honey mesquite models because spatial autocorrelation in shrub cover was high throughout the study, and this structure produced acceptable residual patterns and autocorrelation functions.

Once model assumptions were met, we implemented a two-stage model selection approach that is efficient and reliable (Morin et al., 2020). Stage 1 consisted of fitting fixed effects of herbivore treatment (control [intercept], -B, -BL, -BLR), annual precipitation, current wet season precipitation, current wet season + previous-year wet season precipitation (legacy effects), 5-year SPEI, their stepwise additive effects, herbivore treatment $\times$ precipitation or aridity interactive effects, and a null model using maximum likelihood estimation (Appendix S1: Table S1). We then selected Stage 1 models (difference in Akaike information criterion between models and top model $[\Delta\text{AIC}] < 4$) and fit these models in Stage 2 with an additional fixed effect representing potential interspecific competition (mesquite cover for perennial grass models, perennial grass cover for mesquite models). Honey mesquite models containing wet season precipitation fixed effects were not fit with interspecific competition effects due to multicollinearity between perennial grass cover and wet season precipitation ($r = 0.47$). We identified competitive models ($\Delta\text{AIC} < 2$) in Stage 2 for both perennial grasses and mesquite and assessed these for uninformative parameters (Arnold, 2010). We then refit the final models using restricted maximum likelihood to yield our parameter estimates (Zuur et al., 2009).

Plant diversity and community dynamics

We complemented our analysis of plant functional types using species-level foliar cover data to elucidate plant community dynamics in response to herbivore treatments over time. We conducted permutational multivariate analysis of variance (perMANOVA) using package “vegan” (Ver. 2.6-4; Oksanen et al., 2022) in R. We fit a Bray–Curtis dissimilarity matrix to species foliar cover for each plot by year. We then conducted perMANOVA on the dissimilarity matrix to quantify whether year, herbivore treatment, or their interactions were driving differences in plant community composition. Because our measurements of plant foliar cover were temporally dependent, we specified a time series permutational format that was spatially constrained to herbivore

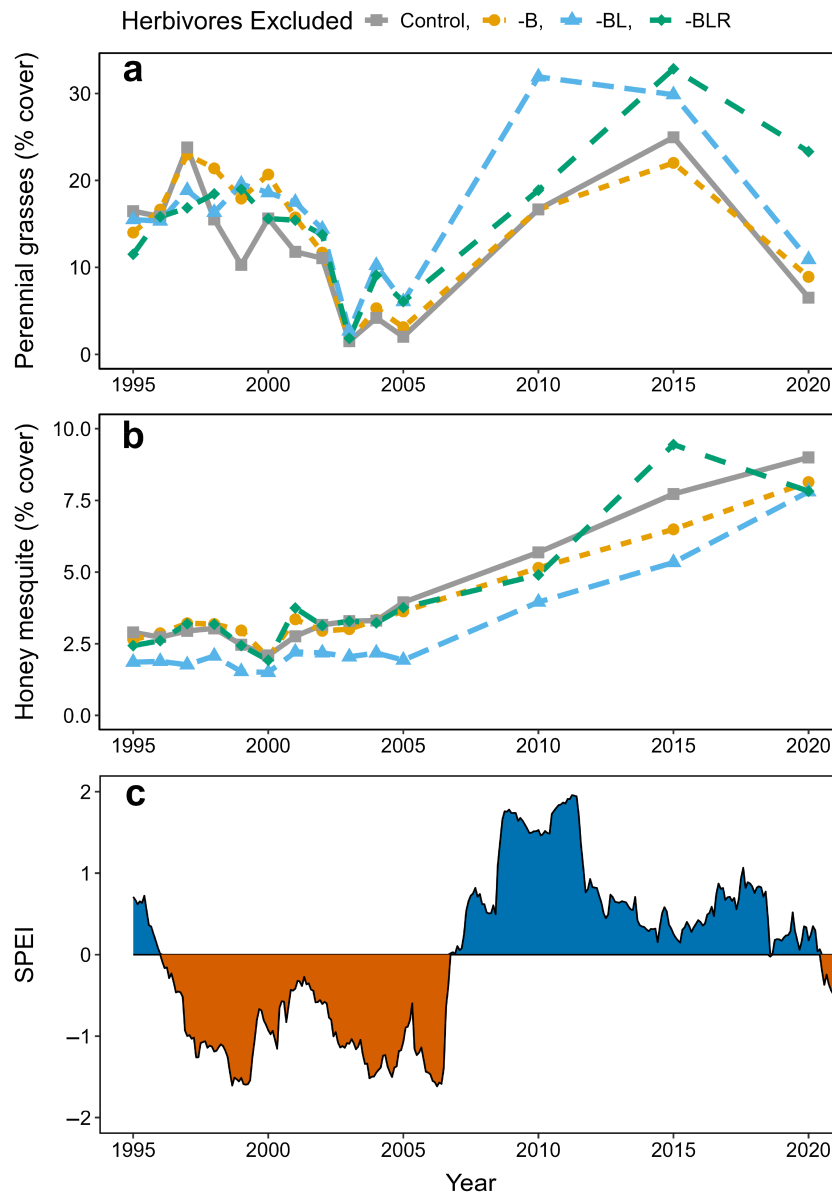


FIGURE 3 Mean percent foliar cover for (a) perennial grasses and (b) honey mesquite from 1995 to 2020 from the herbivore exclusion study at the Jornada Basin Long Term Ecological Research site, New Mexico, USA. Error bars were removed for legibility (see Appendix S1: Figure S5). Treatments included exclusion of bovids (-B), bovids and lagomorphs (-BL), or bovids, lagomorphs, and rodents (-BLR). (c) The Standardized Precipitation-Evapotranspiration Index (SPEI) summed for the previous 60 months is given for each month. Negative SPEI values (red) indicate drier conditions, whereas positive SPEI values (blue) indicate wetter conditions.

treatment plot nested within spatial block. Thus, iterative permutational shuffling was limited to match the spatial and temporal structure of the study. To aid in visualizing perMANOVA results, we conducted nonmetric multidimensional scaling (NMDS) on the dissimilarity matrix, with three reduced dimensions to gauge how herbivore treatments affected plant community composition. We additionally checked model stress to ensure NMDS plots could be reliably interpreted. We then conducted indicator species analysis using package “indicspecies” (Ver. 1.7.12; Cáceres & Legendre, 2009) in R for the early (1995–2005) and late (2010–2020)

periods to identify associations of plant species with herbivore treatments and whether these varied over time.

To provide context for our primary plant community analysis, we fit linear mixed models for plot-level measures of species richness, Shannon diversity, and Pielou’s evenness. Each model included a random intercept for exclosure plot nested within block, an identity variance structure varying per time stratum (Equation 2), and a first-order continuous-time autocorrelation structure (Equation 3). We then fit fixed effects for year, treatment, and year $\times$ treatment using restricted maximum likelihood and applied a marginal *F*-test.

TABLE 1 Results of Stage 2 selection of mixed effects models for responses of perennial grass and honey mesquite cover to mammalian herbivory treatments, climate, and interspecific competition.

Response variable and model parameters	K	ΔAIC	AIC Wt.	LL
Perennial grasses				
Treatment × Ppt (wet season) + Ppt (wet 1-year lag) + SPEI (5-year)	27	0.00	0.57	−677.07
Treatment × Ppt (wet season) + Ppt (wet 1-year lag) + SPEI (5-year) + Competition	28	1.11	0.33	−676.63
Honey mesquite				
Treatment + Ppt (wet season) + Ppt (wet 1-year lag) + SPEI (5-year)	11	0.00	0.75	−501.89
Treatment + Ppt (wet season) + SPEI (5-year)	10	3.57	0.13	−504.68

Note: Models in Stage 1 with $\Delta AIC < 4$ proceeded to Stage 2 (Appendix S1: Table S2) and were fit with additive interspecific competition effects where applicable. Models in bold were refit using restricted maximum likelihood to yield parameter estimates (Appendix S1: Table S4). SPEI is a drought index (Standardized Precipitation-Evapotranspiration Index), and Ppt is precipitation.

Abbreviations: ΔAIC , difference between model AIC and AIC for top model; AIC, Akaike information criterion; AIC Wt., weight of evidence that model is top model; K, number of parameters; LL, log-likelihood.

RESULTS

Cover of perennial grasses and honey mesquite shrubs shifted dramatically over the 25-year experiment (Figure 3). Perennial grasses decreased from 2000 to 2005, with precipitous declines starting in 2003 (Figure 3a) concurrent with the deepening of long-term drought (Figure 3c). A shift to wetter conditions (Figure 3c) spurred variable recovery of perennial grasses among treatments from 2005 to 2015, followed by differential declines from 2015 to 2020. Mean foliar cover of perennial grasses at control plots (accessible to all herbivores) was only 6.5% (SD = 2.5) in 2020 compared to 16.5% (SD = 5.9) in 1995. Conversely, there was a wholesale expansion of honey mesquite cover after 2005 (Figure 3b), which included a threefold increase on control plots from 2.9% (SD = 3.0) in 1995 to 9.0% (SD = 5.4) in 2020. Moreover, occupancy of sampling quadrats by mesquite increased over time (60 quadrats in 1995, 86 in 2005, 120 in 2020), whereas mean height of mesquite decreased from 64.4 cm in 2005 to 42.5 cm in 2020. Collectively, these changes indicated not only growth of existing individuals but also recruitment of new mesquite shrubs following the drought-induced perennial grass collapse.

Annual precipitation was variable (1990–2020: mean = 246 mm, range = 99–407; Appendix S1: Figure S2a) and displayed trends similar to wet season precipitation (1990–2020: mean = 152 mm, range = 28–371; Appendix S1: Figure S2b). Prior to and during the collapse of perennial grass cover in 2003–2005, wet season precipitation was often scarce with 10 years of below average rainfall between 1990 and 2005.

Perennial grasses

Perennial grasses and honey mesquite shrubs responded differently to herbivore exclusion treatments, precipitation, long-term aridity, and interspecific plant–plant competition. For perennial grasses, a single model including treatment × wet season precipitation + previous-year wet season precipitation + SPEI (5-year) was selected in Stage 1 (Appendix S1: Table S2). In Stage 2, the addition of interspecific competition did not improve model fit (Table 1). Thus, perennial grasses displayed interactive effects of herbivore treatments and current-year wet season precipitation; specifically, exclusion effects were most apparent during wet years (Figure 4a, Appendix S1: Table S3). Overall, perennial grasses responded positively to wet season precipitation ($\beta = 0.035$, SE = 0.007). The addition of lagomorph exclusion to bovid exclusion (Treatment -BL) strongly increased grass cover during wet periods ($\beta = 0.027$, SE = 0.009) compared to bovid only exclusion and controls (Figure 4a). The additional exclusion of rodents (Treatment -BLR) did not increase the strength of the treatment × wet season precipitation interaction ($\beta = 0.025$, SE = 0.009). However, rodent exclusion was the only treatment in which perennial grasses not only recovered to initial, pre-drought foliar cover levels but exceeded them by 2020 (Figure 2a). Perennial grasses also responded positively to SPEI ($\beta = 5.36$, SE = 0.56; Figure 4b) and to a legacy effect of previous-year wet season precipitation ($\beta = 0.018$, SE = 0.004; Figure 4c), whereby perennial grass cover saw subsidiary improvement following years with high monsoonal rains.

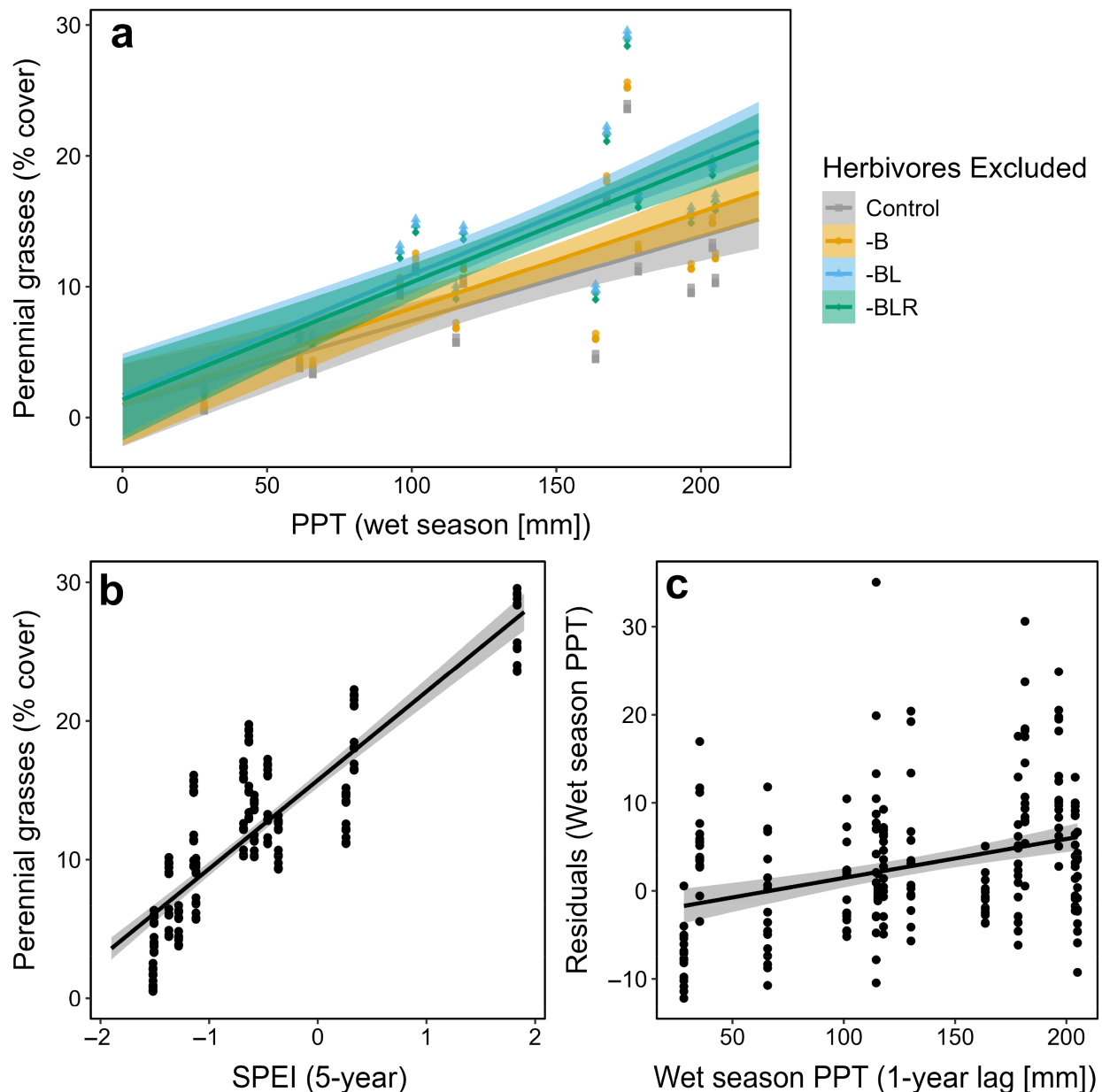


FIGURE 4 Predictive plots from the top linear mixed model for perennial grasses (see Table 1), from 1995 to 2020, at the herbivore exclusion experiment at the Jornada Basin Long Term Ecological Research site, New Mexico, USA. Perennial grass cover responded to (a) herbivore–climate interactions in which current wet season precipitation (PPT) most strongly affected grass cover in plots excluding lagomorphs (-BL and -BLR treatments), (b) aridity measured by a 5-year Standardized Precipitation-Evapotranspiration Index (SPEI), and (c) legacy effects of the previous wet season precipitation. For display purposes, legacy wet season precipitation is illustrated as unaccounted for residual variance from a model including current wet season precipitation as a fixed effect. Shaded regions indicate 95% CIs.

Honey mesquite

In Stage 1 selection for honey mesquite, two models with $\Delta\text{AIC} < 4$ proceeded to Stage 2 (Appendix S1: Table S4). Because both models contained wet season precipitation as a fixed effect, no grass-on-shrub competition effects were fit in Stage 2 (Table 1). Thus, the final model for honey

mesquite contained herbivore treatment + wet season precipitation + previous-year wet season precipitation + SPEI (5-year) (Table 1). However, the addition of herbivore treatment to models with either SPEI or wet season precipitation + legacy effects did not improve model fit (log-likelihood; Appendix S1: Table S4). Thus, treatment was identified as an uninformative parameter.

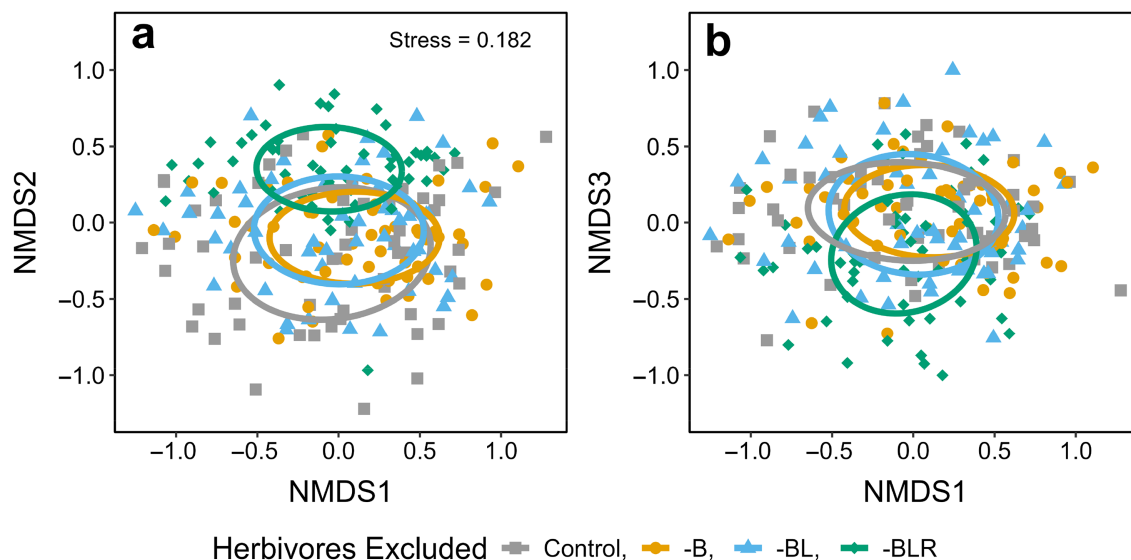


FIGURE 5 Nonmetric multidimensional scaling (NMDS) of plant species foliar cover following hierarchical herbivore exclusion (-B, bovids; -BL, bovids and lagomorphs; -BLR, bovids, lagomorphs, and rodents), from 1995 to 2020, at the herbivore exclosure experiment, Jornada Basin Long Term Ecological Research site, New Mexico, USA. Ellipses represent the 95% CI around the centroid of plant community composition for herbivore treatments and controls. Rodent exclusion resulted in a distinct plant community (see perMANOVA analysis; Appendix S2: Table S1).

This conclusion was supported by the 95% CIs for parameter estimates for the herbivore treatments that all included 0 (Appendix S1: Table S3).

Honey mesquite cover responded positively and strongly to SPEI ($\beta = 1.12$, $SE = 0.17$; Appendix S1: Figure S3). Expansion of mesquite during extended wet periods was ubiquitous across herbivore treatments and controls. Honey mesquite cover also responded negatively to wet season precipitation ($\beta = -0.009$, $SE = 0.003$), however, suggesting potential competitive limitation from perennial grasses that increased during wet years.

Plant diversity and community dynamics

The perMANOVA analysis of plant community composition indicated an herbivore treatment $\times$ year effect ($F = 1.91$, $df = 3$, $p = 0.001$; Appendix S2: Table S1). The NMDS ordination (stress = 0.182) illustrated that the overall treatment effect was due to a separation of plant communities when rodents were excluded (-BLR treatment vs. others; Figure 5). Indicator species analysis further elucidated strong compositional associations among herbivore treatments that varied over time (Appendix S2: Table S2). Key perennial grass species, including *Aristida pansa*, *S. flexuosus*, *S. contractus*, and *Sporobolus cryptandrus*, were associated with rodent exclusion during the dry, early phase of the study, as were numerous perennial forb species (Appendix S2: Table S2a). In contrast, *B. eriopoda* was strongly associated with rodent exclusion plots

following perennial grass recovery in the wet, late phase of the study, as was *Dalea nana* and *Y. elata* (Appendix S2: Table S2b).

In total, we recorded 136 plant species during the study. Species richness decreased over time ($\beta = -1.21$, $SE = 0.056$; Appendix S2: Table S3a, Figure S1a) but was not affected by herbivore exclusion treatments ($F = 3.38$, $p = 0.068$; Appendix S2: Figure S1d). Conversely, Shannon diversity was higher in herbivore treatments excluding rodents ($\beta = 0.46$, $SE = 0.13$; Appendix S2: Table S3b, Figure S1e), but varied considerably by year ($F = 3.24$, $p = 0.023$; Appendix S2: Figure S1b), whereby plots excluding rodents were most diverse in the dry, early phase of the study ($\beta = -0.015$, $SE = 0.008$). Moreover, Pielou's evenness index varied by herbivore treatment over time ($F = 5.24$, $p = 0.001$) such that rodent exclusion treatments were most even in species foliar cover ($\beta = 0.12$, $SE = 0.038$; Appendix S2: Table S3c, Figure S1c), but evenness also declined over time ($\beta = -0.006$, $SE = 0.003$) providing additional evidence of a shift toward honey mesquite and black grama dominance late in the study.

DISCUSSION

Because shrub encroachment is a concern for global drylands (Ding & Eldridge, 2023; Eldridge et al., 2011), it is critical to understand whether herbivores promote grassland–shrubland transitions or broadly alter plant communities. Our 25-year experiment in a Chihuahuan

Desert grassland documented extensive expansion of honey mesquite related to climate but with no evidence of facilitation or inhibition by mammalian herbivores. In contrast, perennial grasses responded to interactions between herbivory by native mammals and climate, with perennial grass cover increasing most when lagomorphs were excluded during wet periods. Rodent exclusion also produced a distinct plant community that was more diverse and had higher evenness. Overall, native mammals more strongly affected plant dynamics than did domestic and exotic bovids.

During an extended dry period early in our study, honey mesquite cover remained stable while perennial grasses declined substantially. Following the collapse of grasses, mesquite expansion was ubiquitous across the site during a subsequent wet period. These trends are consistent with our hypotheses that shrubs are favored over grasses by drought (Gherardi & Sala, 2015; Throop et al., 2012) and that shrubs can experience competitive release from grasses during early stages of encroachment (Pierce, Archer, & Bestelmeyer, 2019).

However, our hypothesis was not supported that large bovids further reduce perennial grass cover during dry periods and trigger shrub encroachment. Cattle and African oryx exclusion provided only a marginal increase in perennial grass cover compared to controls, and mostly during wet periods (Figure 4). This result was surprising given large herbivores affect vegetation dynamics of grasslands and savannas globally (Pringle et al., 2023), with negative impacts on ecosystem services being most pronounced in drylands with warm climates and high precipitation seasonality (Maestre et al., 2022), such as the Chihuahuan Desert. Moreover, large mammalian herbivores are expected to exert stronger per capita and net effects on grassland vegetation relative to small mammals (Pringle et al., 2023). In our study, cattle were grazed at light-to-moderate levels, compared to historically high-intensity grazing, which may have limited their contemporary effects.

After cattle were removed from the site in 2008, oryx did not limit perennial grass recovery during a wet period when oryx abundances were increasing (Andreoni et al., 2021). The effects of invasive ungulates on ecosystem processes may take decades to become apparent following introduction into their nonnative range (Allen et al., 2023). We expect that the oryx population may grow to the point that they have significant effects on remaining black grama grasslands, even in the absence of livestock grazing. Rangeland management aimed at grassland recovery, such as brush management and adaptive grazing, could then prove ineffective in maintaining forage production in regions where oryx are increasing.

In our experiment, large herbivores also did not directly limit or promote mesquite encroachment. In

other shrub-encroached systems, such as Gorongosa National Park in Mozambique, reintroduction of an assemblage of large mammalian herbivores was sufficient to not only limit but reverse encroachment by an invasive shrub, *Mimosa pigra* (Guyton et al., 2020). Cattle and oryx (Cain et al., 2017) also incorporate shrubs into their diet, but neither constrained mesquite cover in our system. Conversely, cattle can disperse honey mesquite seeds potentially leading to higher shrub recruitment (Ansley et al., 2017). However, bovid exclusion did not slow shrub expansion, suggesting the existing seed bank at our site was sufficient to promote shrub encroachment irrespective of dispersal by mammals.

Evidence from three long-term enclosure experiments in Kenya (i.e., KLEE, UHURU, GLADE; Goheen et al., 2010, 2018; Keesing, 2000) indicates that removal of large herbivores could provide a competitive release for smaller herbivores, thus leading to a compensatory response. In our study, excluding domestic cattle, and especially an exotic ungulate such as oryx, may have increased abundances of native lagomorphs and rodents and promoted their strong effects on perennial grass cover (see below). Such a compensatory response from the small herbivores could have dampened the effects of large bovid exclusion. However, because we did not monitor native herbivores within our enclosures, we could not test for the effects of species interactions among herbivore groups related to body size.

As we predicted, perennial grasses responded positively to precipitation across multiple time scales (i.e., current wet season, legacy wet season, 5-year SPEI drought index), and native small herbivores had their greatest effect on perennial grasses during wet periods. Specifically, lagomorphs contributed strongly to the herbivore–climate interaction affecting perennial grass cover, best measured with wet season precipitation. After recovery from the drought-induced collapse, perennial grass cover was two times higher on plots excluding lagomorphs than on plots allowing lagomorph access, until a decline during the last 5 years (Figure 3a). However, foliar cover of black grama, a core perennial grass (Christensen et al., 2023), was approximately three times higher in plots excluding rodents by 2020 (Appendix S2: Figure S2c). Thus, our results indicate Chihuahuan Desert rodents, particularly the dominant kangaroo rats (Lightfoot et al., 2012; Schooley et al., 2018), can reduce cover of perennial grass species with small seeds through graminivory (Kerley et al., 1997; Kerley & Whitford, 2009), in addition to affecting plant community dynamics via selective granivory of large-seeded annual species (Heske et al., 1993; Maron et al., 2021) and soil disturbance from burrowing (Brown & Heske, 1990). Our results differ from a similar experiment in the Chihuahuan Desert at the Sevilleta LTER site in which rodents exhibited minimal top-down control of plant

cover, presumably due to low primary productivity consistently limiting rodent abundances (Báez et al., 2006).

Such grass reductions from native herbivores did not increase the rate of shrub expansion as our site transitioned from a grassland to a mixed life-form savanna. Higher perennial grass cover from exclusion of native mammals, however, could inhibit future state change to a shrubland with very few grasses. Continued monitoring will determine whether this scenario occurs or whether mesquite shrub expansion gradually reduces perennial grass cover irrespective of variations in herbivore pressure (Pierce, Archer, & Bestelmeyer, 2019).

Both rodent and lagomorph herbivory pressure likely increased over our study due to altered habitat structure from the broad-scale shift from grassland toward shrubland. Spatial abundances of Chihuahuan Desert rodents (Schooley et al., 2018) and lagomorphs (Wagnon, 2023), measured across grassland–shrubland gradients, respond positively to monsoonal rains and increased food resources most strongly in shrublands. Lagomorphs also preferentially use mesquite shrublands over grasslands because they perceive this habitat as safer with lower predation risk (Wagnon et al., 2020). These dynamics support the notion that grass seedling herbivory by lagomorphs is greatest in shrublands and grassland–shrubland ecotones (Bestelmeyer et al., 2007), which could have inhibited grass recovery following the drought (Abercrombie et al., 2019; Davies et al., 2023). Thus, shrub encroachment creates an environment that can promote herbivory feedbacks from periodic pulses of native consumers (Appendix S1: Figure S1a). More generally, the collective results for our site support the model for shifting bottom-up and top-down control, proposed for dryland systems in northern Chile (Meserve et al., 2003) and Australia (Letnic et al., 2011), in which wet periods strengthen biotic interactions, including top-down effects of herbivores on perennial grass cover.

Rodents also fundamentally altered the composition, diversity, and evenness of the grassland plant community. However, these rodent effects were strongest early in the experiment during drought (see also Maron et al., 2021) when overall plant diversity was high, likely providing increased scope for selective granivory. Then, as shrubs expanded, plant diversity declined irrespective of rodent exclusion. This outcome supports the general pattern for loss of plant species diversity with shrub encroachment (de Abreu & Durigan, 2011; Ratajczak et al., 2012; Wiczorkowski & Lehmann, 2022), although such global trends depend strongly on the study system and shrub traits (Eldridge et al., 2011). Rodent effects on community composition then became less apparent as our site became increasingly shrub-dominated with reduced diversity. In that encroached state, black grama grass, a former dominant that is in decline regionally,

was a key indicator of rodent exclusion (Appendix S2: Table S2b). These results indicate that rodents can strongly influence the structure and function of desirable grassland plant communities. These effects can be modulated by disturbance, such as extensive drought, and may amplify hydrological and soil feedbacks that can reinforce grassland loss and shrub establishment and persistence (D’Odorico et al., 2011).

Overall, our results demonstrate the importance of monitoring both native and managed mammalian herbivores and their interactions with climate in studies of grassland–shrubland transitions in drylands. Landscape change was governed by the overriding influence of climate during dry periods, whereas lagomorphs and rodents exhibited top-down effects on perennial grasses during wet periods. Our field experiment also highlights the critical role of very long-term studies in ecology (Hughes et al., 2017). If we had stopped sampling after 10 years, we would have concluded that herbivores had no control on perennial grass cover and that shrub cover was static. The longer time frame enabled us to unveil climate-sensitive dynamics that may apply to global drylands undergoing grassland–shrubland transitions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Datasets are available through the Environmental Data Initiative’s EDI Data Portal as follows: quadrat vegetation cover data (Lightfoot & Bestelmeyer, 2022), <https://doi.org/10.6073/pasta/7c9e83391e3000acbb86503925385713>; precipitation data for IBP station from 1990 to 2012 (Thatcher & Bestelmeyer, 2023), <https://doi.org/10.6073/pasta/caae15334e7707af04bb761c14079e57>; precipitation data for G-IBPE station from 2013 to 2020 (Anderson, 2022a), <https://doi.org/10.6073/pasta/7b5213c7c6d46e621312abfb3906388b>; daily temperature summaries from 1990 to 2020 (Anderson, 2022b), <https://doi.org/10.6073/pasta/540b5ec723639017c9faa65e3b1fc142>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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