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Shrub encroachment promotes positive feedbacks from herbivores that reinforce ecosystem change

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Abstract

Herbivores can be drivers of ecosystem change by triggering and reinforcing vegetation transitions. Such processes may be prevalent in drylands with low productivity where herbivore abundances are linked to climate-driven resource pulses. In the Chihuahuan Desert, ecosystems are being transformed from black grama (*Bouteloua eriopoda*) grasslands to honey mesquite (*Neltuma* [formerly *Prosopis*] *glandulosa*) shrublands. Domestic livestock, exotic African oryx (*Oryx gazella*), and native rodents and lagomorphs have all been implicated as drivers of these transitions through multiple mechanisms affecting different plant life stages. Across shrub encroachment gradients, we paired a long-term (21 years) herbivore exclusion experiment focused on established perennial grasses with field trials measuring herbivory risk for perennial grass seedlings. We evaluated the roles of cattle, oryx, and native herbivores in reducing grass cover, and tested whether herbivore effects on grass cover and seedling mortality varied among ecosystem states (grassland, ecotone, and shrubland). Cattle and African oryx did not contribute strongly to vegetation dynamics. However, long-term exclusion of rodents and lagomorphs led to two-to-threefold increases in perennial grass cover compared to control plots (with open access to all herbivores) in shrub-encroached states where mesquite shrubs provided these herbivores with cover from predators. Likewise, herbivory of perennial grass seedlings was highest in the shrub-encroached states and was driven by rodents. Our results indicate that native rodents and lagomorphs exert strong control over perennial grass dynamics, creating positive feedbacks mediated by changes in habitat structure that can reinforce grassland–shrubland transitions in drylands.

KEYWORDS
African oryx, Chihuahuan Desert, desert rodents, drylands, ecosystem change, grassland ecology, herbivory, shrub encroachment

INTRODUCTION

Herbivores strongly influence ecosystem change and restoration globally (Kamaru et al., 2024; Lundgren et al., 2020; Xu et al., 2023). However, herbivore effects on ecosystems remain difficult to predict because herbivore–plant interactions are mediated by external drivers, especially climate (Andreoni et al., 2024), which can lead to unexpected ecosystem changes (Hawkes & Sullivan, 2001; Maron et al., 2014). Moreover, herbivores can alter ecosystems through multiple processes including selectively consuming plants (Brown & Heske, 1990; Maron et al., 2021) and disturbing soils (Davidson et al., 2012; Nickell et al., 2018). These processes may affect different plant life stages (Rasmussen & Yang, 2023; Warner & Cushman, 2002), and they may be amplified by ecosystem changes that create positive feedbacks.

Drylands are especially at risk of ecosystem transformation because herbivore–climate interactions can drive abrupt shifts in vegetation in these low-productivity systems (Berdugo et al., 2022; Bestelmeyer et al., 2011; Gaitán et al., 2018). Encroachment of honey mesquite (*Neltuma* [formerly *Prosopis*] *glandulosa*) shrubs into black grama (*Bouteloua eriopoda*) grasslands in the Chihuahuan Desert is an unequivocal example of ecological state transitions in drylands (D'Odorico et al., 2011). The current model for these grassland–shrubland transitions emphasizes historical triggers from drought and livestock overgrazing; additional drivers including precipitation variability, increased atmospheric CO_2, and spatial contagion; plus feedbacks from reduced fire and redistribution of soil and nutrients (Bestelmeyer et al., 2018). Furthermore, native lagomorphs (Abercrombie et al., 2019; Bestelmeyer et al., 2007) and rodents (Brown & Heske, 1990; Kerley & Whitford, 2009), domestic cattle (Havstad et al., 2006), and exotic African oryx (*Oryx gazella*, Andreoni et al., 2021) have been implicated as drivers.

Herbivores could reduce grass cover and encourage shrub dominance via multiple mechanisms. Perennial grasses can restrict the growth rate of mesquite shrubs, presumably via belowground competition for soil water, until shrubs become large (Pierce et al., 2019). Thus, removal of grasses by herbivores could favor survival and expansion of shrubs. Herbivory and soil disturbance by mammals also could increase bare ground, reduce structural connectivity, and alter the transport of soil and nutrients by wind and water (Okin et al., 2015; Peters et al., 2020). Such redistribution of resources from interspaces to shrubs could reinforce conditions unfavorable for grasses and promote islands of fertility under shrubs (Allington & Valone, 2014; Schlesinger et al., 1990). Furthermore, removal of remnant grasses by mammalian herbivores in shrub-dominated states could decrease the opportunity for state change reversal, which is rare but possible during and after extended wet periods (Peters & Savoy, 2023).

It remains unclear, however, whether mammalian herbivores mainly act as *triggers* of transitions from grassland to shrubland states, or as *feedbacks* that reinforce shrub encroachment (Abercrombie et al., 2019; Bestelmeyer et al., 2007). A trigger role would be indicated by high levels of grass defoliation or seedling herbivory within a grassland state that could create conditions favorable for shrub recruitment and survival (Pierce et al., 2019). A feedback role would be indicated by high levels of herbivory in shrub-encroached states producing conditions that accelerate grass loss and shrub dominance. Such feedbacks are possible if herbivore pressure is elevated with increasing shrub cover. It is likely that trigger versus feedback roles vary among different herbivore groups.

Shrub encroachment could alter the pressure of herbivore groups in several ways. First, herbivore abundances change across shrub encroachment gradients (Hernández et al., 2005). For example, African oryx are more abundant in unencroached grassland habitats, especially during dry periods (Andreoni et al., 2021) when grasslands are most vulnerable to transformations (Gherardi & Sala, 2015). In contrast, the biomass of Chihuahuan Desert rodents varies among ecological states depending on monsoonal rains, but rodents obtain higher biomasses on shrub-encroached sites when their populations irrupt (Schooley et al., 2018). Likewise, lagomorph abundances are greater on shrublands than grasslands during wet periods when their numbers are high (Wagnon et al., 2024). Second, shrub encroachment could alter the landscape of fear for herbivores by providing habitat with lower perceived predation risk and increased foraging opportunities (Loggins et al., 2019). Many nocturnal desert rodents behave as if shrub microhabitats are safer than open microhabitats (Bowers, 1988; Kelt, 2011; Kotler et al., 1991; Thompson, 1987). Similarly, desert lagomorphs perceive habitats with high shrub cover to have lower predation risk (Camp et al., 2012; Wagnon et al., 2020), and they consume more food under shrubs than in open areas (Longland, 1991). Lastly, shrub canopies should provide smaller herbivores with greater protection from solar radiation compared to open grasslands (Kustas et al., 2000), especially for lagomorphs with crepuscular peaks in activity (Arias-Del Razo et al., 2011). Such a shift in the thermal landscape (Nowakowski et al., 2018) may allow lagomorphs to increase their time spent foraging in shrublands while using shrub canopies for thermoregulation. Thus, multiple changes in the abundance or behavior of small herbivores could generate feedbacks that reinforce shrub-encroached states in drylands.

Detecting herbivory effects has been challenging, however, especially over short timescales (i.e., <10 years; Báez et al., 2006). For example, Svejcar et al. (2019) found that excluding rodents and lagomorphs across grassland–shrubland gradients in the Chihuahuan Desert had no effect on black grama recovery from disturbance over 8 years. Yet, long-term studies demonstrate that herbivory effects from native mammals, whose populations are strongly linked to climate, may take a decade or more to become apparent (Andreoni et al., 2024). Likewise, long-term studies in other drylands have revealed delayed effects of herbivore treatments on herbaceous vegetation such as occurred in the Kenya Long-term Exclosure Experiment (KLEE; Riginos et al., 2024).

Our first objective was to measure long-term influences of multiple herbivore taxa on perennial grass cover and recovery across a shrub encroachment gradient. Thus, we resampled plots established by Svejcar et al. (2019) in 2001 to test whether effects on perennial grasses were evident after 21 years of herbivore exclusion. Our second objective was to determine if grass seedling survival was related to habitat structure and herbivore abundances across the same encroachment gradient. Moreover, because lagomorph populations in the Chihuahuan Desert have been severely reduced since 2020 due to the rabbit hemorrhagic disease virus (Asin et al., 2021), we examined whether seedling mortality remained higher on shrub-encroached states (Bestelmeyer et al., 2007) when a major consumer group was decimated by a disease outbreak.

We predicted that effects from domestic cattle and exotic oryx would be focused on established perennial grasses in grasslands (Andreoni et al., 2021), acting as potential triggering mechanisms. In contrast, we predicted that long-term exclusion of native rodents and lagomorphs would increase perennial grass cover mainly in shrublands (Abercrombie et al., 2019; Bestelmeyer et al., 2007), where both rodents and lagomorphs obtain their highest abundances after precipitation pulses (Schooley et al., 2018; Wagnon et al., 2024) and habitat structure provides cover from predators (Wagnon et al., 2020) and shade. We also expected that the influence of habitat structure would scale down to microhabitats (Kotler et al., 1991; Thompson, 1987), with nearby shrubs increasing seedling mortality from rodents. Such outcomes would indicate that rodents and lagomorphs reinforce shrub encroachment via positive feedbacks.

METHODS

Study area and sampling design

The Jornada Basin Long Term Ecological Research (JRN LTER; 32°35′ N, 106°51′ W; 1334 m above sea level [asl]) site typifies encroachment by honey mesquite shrublands into black grama grasslands occurring across the northern Chihuahuan Desert (D'Odorico et al., 2011; Figure 1a). The 100,000-ha site includes the New Mexico State University Chihuahuan Desert Rangeland Research Center (CDRRC) and the United States Department of Agriculture Jornada Experimental Range (JER). Both grasslands and mesquite shrublands occur on loamy sand-to-sandy loam soils within the basin. From 1858 to 1998, estimated grassland cover dwindled from 67% to 3% while honey mesquite shrublands expanded from 15% to 59% cover (Peters et al., 2012). Remaining grasslands are frequently dominated by black grama together with dropseed and alkali sacaton (*Sporobolus* spp.) and tobosa (*Pleuraphis mutica*; Christensen et al., 2023), and commonly, host cholla (*Cylindropuntia* spp.), prickly pear (*Opuntia* spp.), soaptree yucca (*Yucca elata*), longleaf jointfir (*Ephedra trifurca*), and numerous perennial and annual forbs (Peters & Gibbens, 2006). Most of the annual rainfall (mean = 23 cm, range = 10–40 cm) occurs during the monsoon season from July to September (mean = 18 cm, range = 7–27 cm), which is driven by the El Niño-Southern Oscillation (Peters et al., 2012) and Pacific Decadal Oscillation (Christensen et al., 2023).

In 2001, the Ecotone Study was established to examine how shrub encroachment alters dynamics of mammalian consumers, trophic interactions, and their feedbacks to ecosystem state change (Bestelmeyer et al., 2007; Schooley et al., 2018; Svejcar et al., 2019; Wagnon et al., 2020, 2024). Three spatial blocks (i.e., CDRRC Pasture 3; JER Pastures 9 and 12A; Figure 1b) were established with each containing three ecosystem states (3 ha each; 100 × 300 m) representing typical shrub encroachment gradients: grassland, ecotone, shrubland (Figure 1c–e). States within spatial blocks were typically located 200–500 m from adjacent states.

To characterize each state, we used line-point-intercept sampling to estimate percent plant foliar cover (Herrick et al., 2005) over five, 50-m transects with 25-cm intervals ($n = 200$ points per transect). Due to ongoing shrub encroachment since the study was initiated, the ecotone states had shrub cover (mean = 12.5%) similar to shrubland states (mean = 14.0%) by 2021 (Figure 2). However, ecotone states retained greater perennial grass cover and less bare ground than shrubland states (Figure 2). We used this contrast to explore whether shrub or grass cover played the stronger role in herbivory

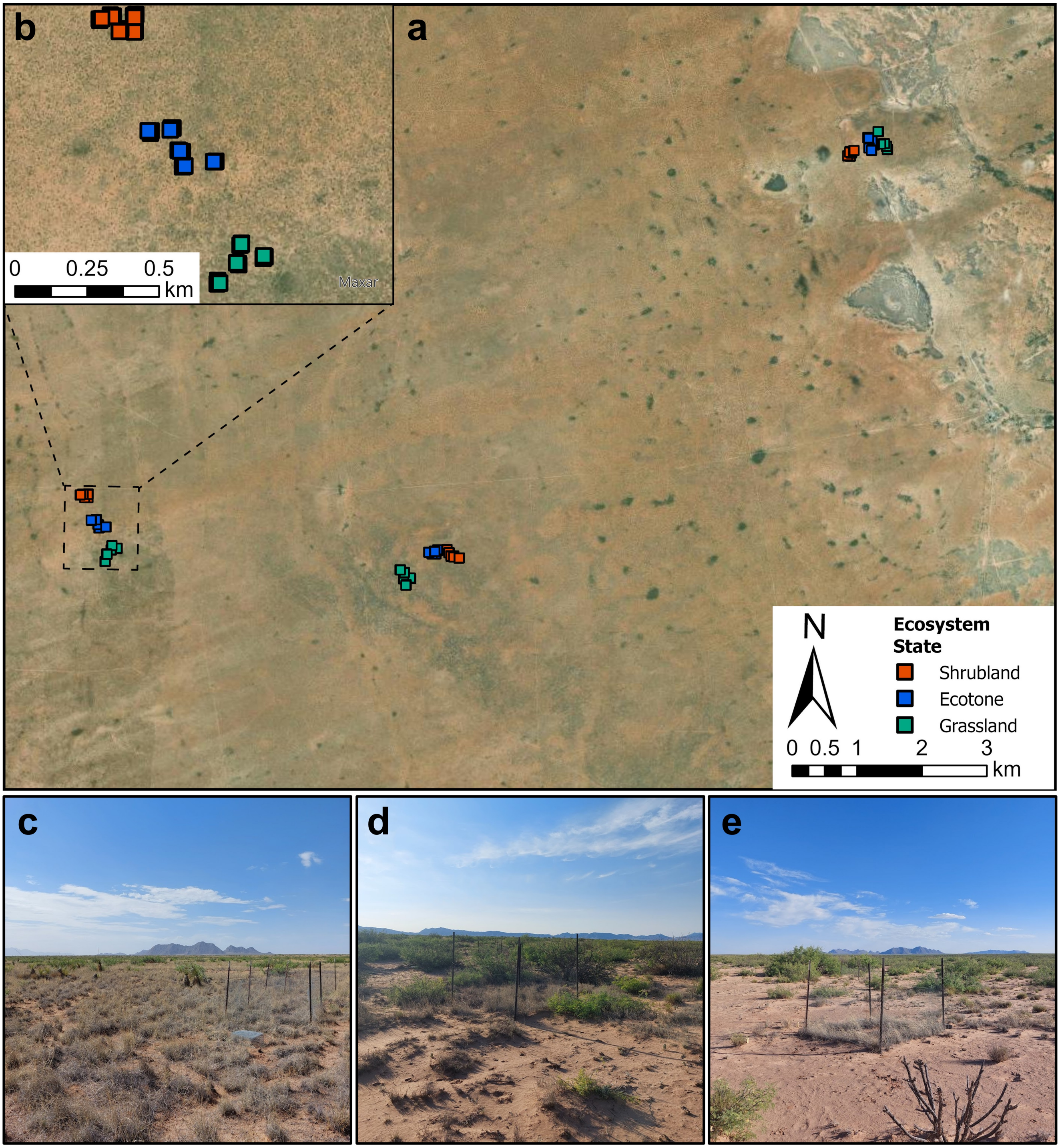

FIGURE 1 (a) The Ecotone exclosure experiment includes clusters containing large herbivore treatment plots (cattle and oryx excluded), full treatment plots (cattle, oryx, lagomorphs, rodents excluded), and control plots (no mammals excluded) established across a shrub encroachment gradient at the Jornada Basin Long Term Ecological Research Site, New Mexico, USA. (b) Clusters including treatment and control plots within one spatial block. (c–e) Examples of 4-m^2 full exclosure plots that were replicated across (c) grassland, (d) ecotone, and (e) shrubland states. The study was initiated in 2001; photographs are from July 2023. Photo credit: Kieran Andreoni.

dynamics across ecological states. Our focal species, black grama, accounted for a mean of 64.1% of all perennial grass cover, whereas honey mesquite accounted for most perennial shrub cover (mean = 93.3%; Appendix S1: Figure S1).

Mammalian herbivores

The mammalian herbivore community included domestic cattle, exotic African oryx, native lagomorphs, and native rodents. Cattle stocking on two spatial blocks of

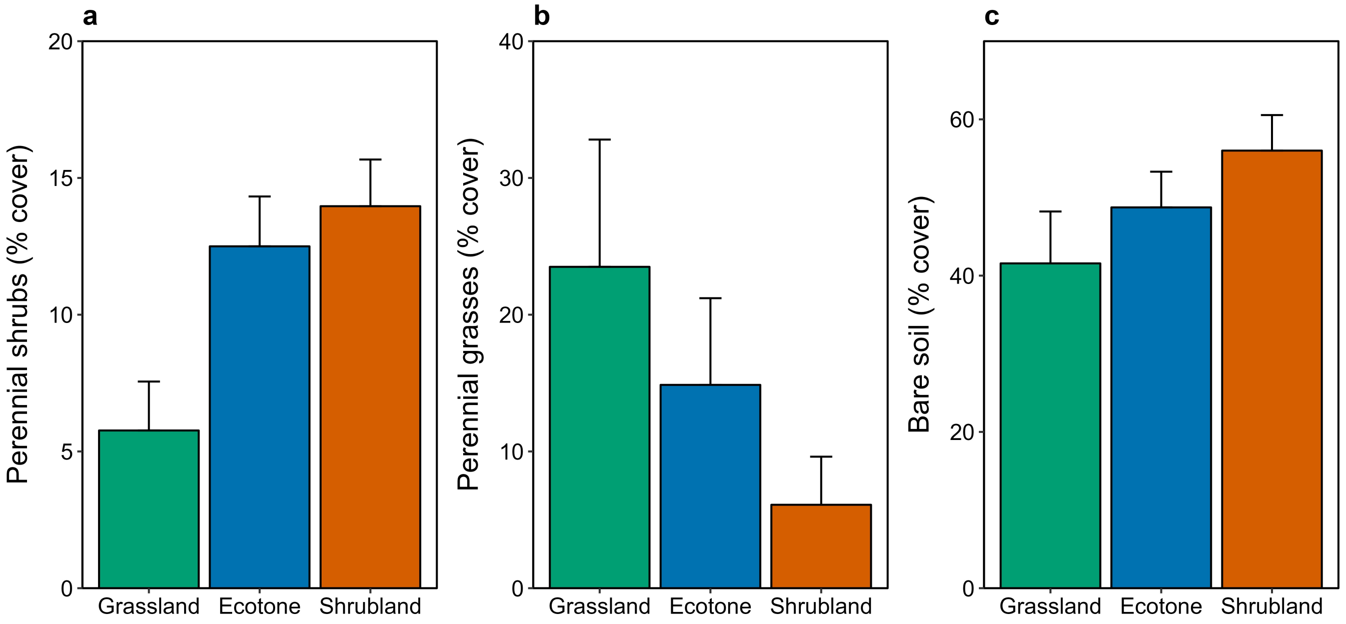

FIGURE 2 Percent foliar cover of (a) perennial shrubs, (b) perennial grasses, and (c) bare soil across grassland, ecotone, and shrubland ecosystem states in 2021 on the Ecotone exclosure experiment, Jornada Basin Long Term Ecological Research Site, New Mexico, USA. Bars represent means for percent foliar cover +1 SE.

the Ecotone Study (Pasture 3 and Pasture 12A) was intermittent and light-to-moderate in intensity, whereas cattle grazing was removed entirely from Pasture 9 in 2008 (Havstad & Bestelmeyer, 2019). Conversely, oryx abundances have been increasing regionally since their introduction to the Chihuahuan Desert (Bender et al., 2019) and at our site since 2014 (Andreoni et al., 2021). Native lagomorphs included the black-tailed jackrabbit (*Lepus californicus*) and desert cottontail (*Sylvilagus audubonii*). The rodent community (Schooley et al., 2018) consisted of a diverse assemblage of species and feeding strategies (Hope & Parmenter, 2007) including granivorous kangaroo rats (*Dipodomys* spp.) and pocket mice (*Chaetodipus eremicus*, *Perognathus flavus*), folivorous woodrats (*Neotoma leucodon*, *N. micropus*) and spotted ground squirrels (*Xerospermophilus spilosoma*), and omnivorous mice (*Onychomys* spp., *Peromyscus* spp.).

Long-term herbivore exclosure experiment

In 2001, five clusters of plots were established at each of the nine states ($n = 45$ clusters; Svejcar et al., 2019) with each cluster containing two herbivore-exclusion treatment plots and an unfenced control plot (Figure 1). Clusters were located in patches dominated by black grama with ≥75% vegetation cover. Treatment plots included a 2 × 2-m full exclosure (no mammal access), a large mammal exclosure (lagomorph and rodent access), and unfenced controls (cattle, oryx, lagomorph, and rodent access). Full exclosures were 1 m tall and constructed with 2.5-cm wire mesh, with an additional 20 cm of mesh buried belowground to prevent small mammal burrowing, and out-curving at the top to deter rodent climbing. Large mammal exclosures were structurally similar to full exclosures, but two of the four sides had approximately 2 × 0.5-m (L × H) entries at the ground level to allow rodent and lagomorph access. Fencing above the entries excluded large mammal access. Treatment and control plots within clusters were typically separated by 2–5 m.

In 2001, plant aboveground biomass was physically removed (i.e., resulting in 0% black grama cover and 100% bare ground cover) from a 40 × 40-cm subplot at the center of each treatment and control plot. Then, black grama recruitment and recovery from the disturbance were assessed in relation to herbivore exclusion treatments from 2002 to 2008 (Svejcar et al., 2019). We examined whether the absence of herbivore effects in that study was due to its limited duration (i.e., 8 years). In September 2022, following monsoon rains, we resampled perennial grass recovery from disturbance and total percent foliar cover of perennial grasses across treatment and control plots to test whether the longer time frame (i.e., 21 years since establishment) revealed herbivory effects across the shrub encroachment gradient. We estimated percent cover of perennial grasses with four 1 × 1-m vegetation quadrats, strung with a grid of masonry twine at 10-cm intervals (100 10 × 10-cm cells, 1 cell = 1% foliar cover), with each quadrat covering one-fourth of the area of the plot. We then averaged cover estimates for the four quadrats to attain mean perennial grass cover for each 2 × 2-m treatment and control plot (Andreoni et al., 2025a). We additionally followed up on perennial grass recovery from disturbance (Svejcar et al., 2019) with four measurements of perennial grass cover within the disturbed, central subplots using a 20 × 20-cm (2 × 2 cells, 1 cell = 25% foliar cover) subsection of vegetation quadrats with quadrat subsections covering one-fourth of the subplot area. Metal stakes delineating opposing corners of disturbed subplots were established in 2001 and used to orient sampling during our follow-up estimates in 2022. We averaged cover estimates for the four subsamples to attain mean perennial grass cover in disturbed subplots (Andreoni et al., 2025a).

Statistical analysis: Exclosure experiment

To test whether long-term herbivore effects on current grass cover and grass recovery varied by treatment and ecosystem state, we implemented linear mixed-effects models in R (ver. 4.3.2; R Core Team, 2023) using package *nlme* (Pinheiro et al., 2022). Each model contained a random intercept for experimental cluster nested within spatial block. We also included a variance structure per spatial block to resolve residual heterogeneity present in our models (Zuur et al., 2009). For total cover of perennial grasses within plots, and perennial grass cover within disturbed subplots, we fit separate models with fixed effects for herbivore treatment plot (control [intercept], large herbivore exclosure, and full exclosure), ecosystem state (grassland [intercept], ecotone, and shrubland) and their interactive effects, and applied a marginal *F*-test. If interaction terms were not significant, we refit a mixed model with only additive herbivore treatment and ecosystem state fixed effects using restricted maximum likelihood to yield our parameter estimates.

Grass seedling herbivory experiment

We paired the Ecotone exclosure experiment with survival trials for perennial grass seedlings in 2023 following established methods (Bestelmeyer et al., 2007). We grew grass seedlings in a greenhouse environment to ensure high germination success. We used blue grama (*B. gracilis*) for trials, a species native to JRN LTER, because black grama has poor germination rates under controlled conditions. In contrast, blue grama seeds germinate quickly (2–6 days) and readily (64%–100% germination rate) at constant temperatures between 16 and 27°C (Sabo, 1979), and they are morphologically and phylogenetically similar to black grama (Peterson et al., 2015).

We conducted subsequent field trials with seedlings during July–August to mimic the phenology of natural seedling germination following monsoon rains. Seedling experiments were conducted simultaneously within grassland, ecotone, and shrubland states at each spatial block. We established a 28 × 28 × 6-cm (L × W × H; 5 × 5 cells) tray of seedlings at each exclosure cluster ($n = 45$ seedling trays total). Trays were buried at the ground level and placed 1 m north of unfenced control plots. Most trays included 25 seedlings (88%), but in the remaining trays, only 22–24 seedlings germinated. Trials lasted 15 days, and we recorded seedling mortality from herbivory during repeat visits every 3–4 days (Andreoni et al., 2025b). All seedlings were watered on day three of field trials to reduce seedling mortality from desiccation. To gauge the effects of local microhabitat structure on grass seedling survival, we used 1 × 1-m (100 cells, 1 cell = 1% foliar cover) quadrats to estimate shrub cover directly to the east and west of seedling trays and then averaged cover estimates across these two quadrats (Andreoni et al., 2025b).

We initially paired each seedling tray with another tray that allowed access only to rodents and excluded other mammalian herbivores (Andreoni, 2024). However, we found no effect of this treatment, presumably because lagomorphs were scarce due to the epidemic, indicating that rodents were the main consumers of seedlings during trials. So, we focused our analysis on the herbivory of seedlings from the trays with open access to all mammal taxa.

Mammalian herbivore abundances

We estimated the relative abundances of herbivores to quantify herbivore pressure across the shrub encroachment gradient. For cattle, oryx, and lagomorphs, we used a network of camera traps to estimate relative abundances (Andreoni et al., 2021; Schooley et al., 2024; Wagnon et al., 2024). From mid-July to mid-October in 2023, two unbaited cameras (Bushnell Trophy Cam, model number 119436) were deployed at each state (196-m spacing between camera trap stations). Cameras were set to trigger in 3-photo bursts following motion or infrared detection. For each species at a camera station, we considered 60 min between detections as temporally independent. We then summed independent detections for each species at each state, combined across the two camera stations, and divided by the number of trap-nights (i.e., number of 24-h periods in which cameras were active; sampling effort) to yield a metric of photographic rate. This measure of relative abundance is generally correlated with estimates of density (Burton et al., 2015; Kenney et al., 2024). Cattle stocking rates varied within and among years with pastures being grazed based on range condition and restoration objectives, but generally aimed at <30% forage utilization. Cattle were undetected during our 2023 sampling period (but infrequently present on all sites since 2001), so we focused on oryx as the primary bovid in seedling survival analyses. Likewise, desert cottontails were absent in 2023, so we focused on black-tailed jackrabbits for lagomorphs.

For rodents, we used the summed mass (in grams) of captured individuals per hectare from a standardized livetrapping protocol to attain a measure of rodent biomass for each ecosystem state (Bestelmeyer & Schooley, 2022; Appendix S1: Table S1). In October 2023, rodent livetrapping was conducted at each state using a 6 × 16 grid ($n = 96$ traps; Sherman model XLKR baited with oats; NMSU IACUC Protocol number 2309000636) with 20-m spacing between traps (Schooley et al., 2018). We included only species whose diets include nontrivial amounts of green plant tissues (Appendix S1: Table S2) and excluded other species (e.g., some obligate granivores and omnivores; Hope & Parmenter, 2007). Of rodents included as potential seedling predators, we grouped species by their dietary functional type as folivores (*Neotoma* spp., *Xerospermophilus spilosoma*), medium granivores that are also graminivores (*Dipodomys merriami*, *D. ordii*; Kerley & Whitford, 2009), large granivores (*D. spectabilis*), or omnivores (*Peromyscus* spp.).

Statistical analysis: Seedling herbivory

To estimate the survival of perennial grass seedlings across the shrub encroachment gradient, we employed a mixed-effects Cox proportional hazards model using the package *survival* (ver. 3.4-0; Therneau, 2022) in R. We included a random intercept for spatial block, and a fixed effect for ecosystem state (grassland [baseline], ecotone, and shrubland). We used the hazard ratio (HR) to estimate changes in the risk of seedling mortality from herbivory across states, where $HR > 1$ indicated percentage increases in the risk of mortality from herbivory, and $HR < 1$ indicated decreased risk in mortality from herbivory, compared to the baseline.

To identify causal pathways among multiple, interdependent factors, we tested a set of hypothesized relationships among habitat structure, herbivores, weather, and their subsequent effects on seedling mortality using a structural equation model (SEM; Figure 3a). We used a piecewise SEM approach to construct our models in the package *piecewiseSEM* (version 2.3.0; Lefcheck, 2016) in R. We characterized the shrub encroachment gradient using state-level estimates of perennial shrub cover (Figure 2a). We used shrub cover directly adjacent to seedling trays to assess microhabitat effects hypothesized to increase small mammal foraging (Thompson, 1987). We included precipitation during the two-week seedling survival trials (Appendix S1: Figure S2; Anderson, 2023a, 2023b; Duniway, 2023) because rainfall could prompt the emergence of natural seedlings (Peters, 2000) and increase herbivore foraging activity (Levy et al., 2016). For herbivore taxa, we used our state-level estimates of relative abundance for each group (i.e., rodent biomass [Appendix S1: Figure S3]; jackrabbit and oryx photographic rate [Appendix S1: Figure S4]). Our primary response variable was the proportion of seedlings within trays that experienced mortality from herbivory by the end of the trials.

Before constructing SEMs, we first fit models individually for hypothesized paths and inspected parameter estimates and standardized residuals to ensure model fit (Zuur et al., 2009). We used generalized linear models with a normal distribution and identity link function for rodent biomass and oryx abundance as response variables, and a binomial distribution and logit link function for proportional seedling mortality as the response variable using package *lme4* (version 1.1.32; Bates et al., 2015) in R.

For the SEMs, we modeled the influence of ecosystem state (state-level shrub cover) on rodents and oryx to examine how broad-scale habitat structure affected consumer abundances (Figure 3a). Because lagomorphs were scarce in 2023 and had not recovered from the disease-induced decline, we did not model a link between shrub cover and their abundances. Moreover, we initially modeled microhabitat shrub cover as a function of ecosystem state, but ultimately excluded this pathway from our SEMs because these variables were not strongly correlated within our dataset ($R = 0.24$, $p = 0.11$). We included a direct pathway from precipitation during field trials to seedling mortality (Figure 3a).

To explore whether certain rodent functional groups were driving trends in seedling mortality, we fit separate SEMs using three rodent metrics: (1) folivore biomass, (2) folivore plus medium granivore biomass, or (3) total rodent biomass including all relevant functional groups (Appendix S1: Table S2). The three SEMs using alternate metrics for rodent biomass were compared during the last stage of model selection.

We fit our initial SEMs (Figure 3a) including the above relationships and used tests of directed separation to discern whether unspecified links should be included as either explicit pathways or correlated errors to improve

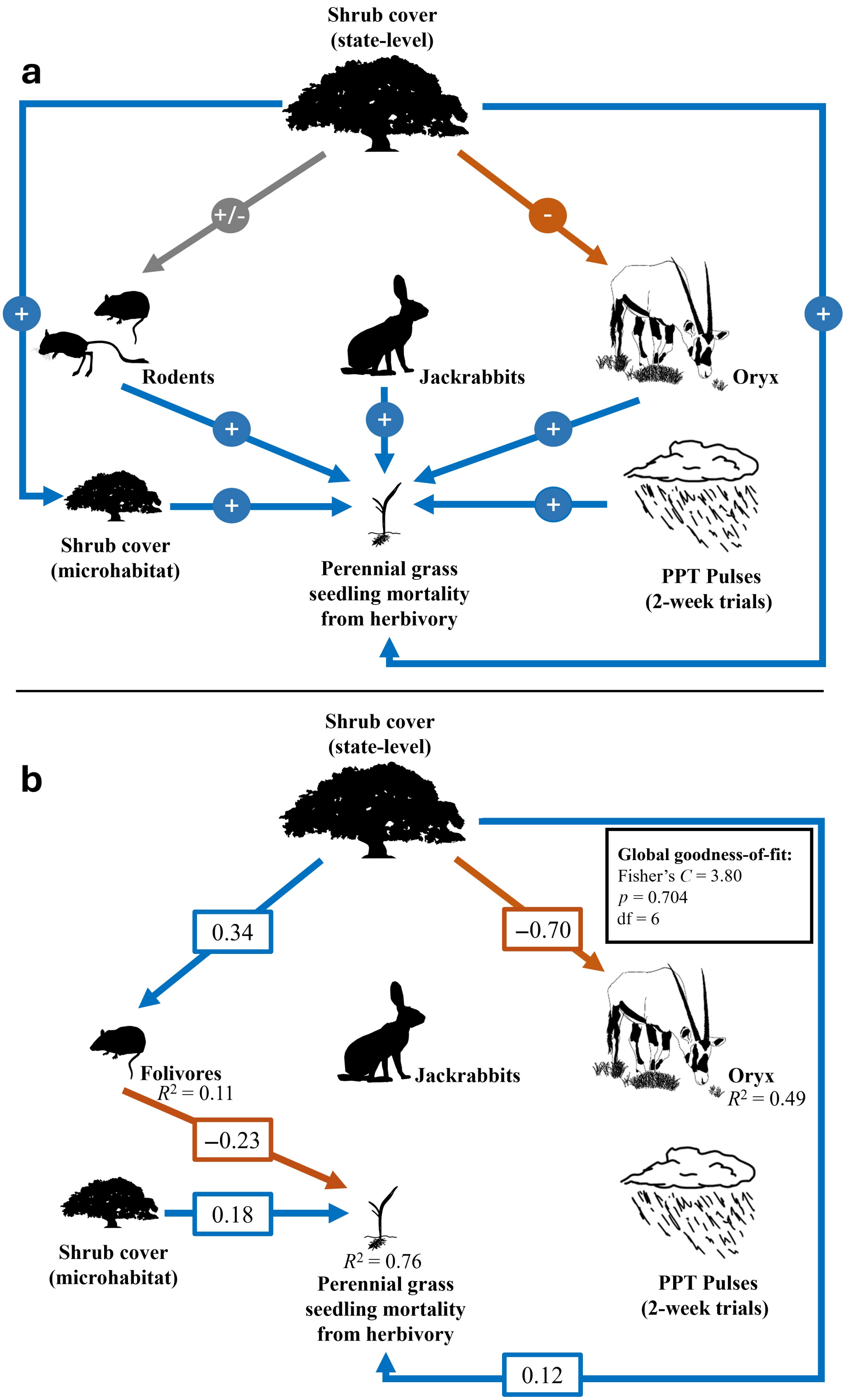

FIGURE 3 Legend on next page.

the SEM's global goodness of fit. We assessed global goodness of fit using Fisher's C and considered models as having adequate fit when $p > 0.05$ (Lefcheck, 2016). We then assessed whether fixed terms in the SEM were significant and removed those with $p > 0.05$ to produce a more parsimonious model. Finally, we compared fit across the three SEMs that included alternate rodent biomass metrics using Fisher's C in which the model with the greatest global p value was selected as the top model.

RESULTS

Long-term herbivore exclosure experiment

The effects of long-term herbivore exclusion on perennial grass cover differed among ecosystem states ($F = 6.62$, $p < 0.001$; Appendix S1: Table S3). Full exclosure plots denying access to all mammalian herbivores, including rodents and lagomorphs, had greater increases in grass cover compared to control plots in shrubland ($\beta = 14.31$, SE = 2.85) and ecotone ($\beta = 6.89$, SE = 2.85) states relative to grasslands (Table 1, Figure 4a). Thus, the effects of excluding rodents and lagomorphs on grasses were strongest where shrub cover was highest across the encroachment gradient. For the ecotone state, mean foliar cover of perennial grasses in controls was 14.2% (SD = 12.9) compared to 29.7% (SD = 24.7) in full exclosures (Figure 4a). For the shrubland state, mean foliar cover of perennial grasses in controls was 6.4% (SD = 9.9) compared to 19.3% (SD = 10.2) in full exclosures.

For perennial grasses in subplots recovering from past disturbance (i.e., 0% perennial grass cover in 2001), there was no ecosystem state × herbivore treatment interaction ($F = 1.44$, $p = 0.229$; Appendix S1: Table S3). However, herbivore treatment was a predictor of recovery ($F = 3.06$, $p = 0.052$), so we refit a mixed model with additive ecosystem state and herbivore treatment effects (Table 1). Positive grass recovery and recruitment into disturbed patches was highest in treatments excluding rodents and lagomorphs (Figure 4b; $\beta = 4.13$, SE = 1.67). By 2022, perennial grass cover had recovered to 4.2% ± 0.7% (mean ± SD) on control plots compared to 12.2% ± 2.9% in full exclosures (Figure 4b).

TABLE 1 Results of linear mixed-effects models for perennial grass cover within herbivore exclosures and controls, and for disturbed subplots within the center of exclosures and controls, across shrubland, ecotone, and grassland ecosystem states.

Response			
Predictors	**β**	**SE**	**95% CI**
Exclosures			
(Intercept: Grassland, control)	22.97	7.77	7.74, 38.20
Ecosystem state			
Ecotone	−7.66	3.33	−14.19, −1.13
Shrubland	−12.43	3.33	−18.96, −5.90
Treatment			
Large herbivores	−0.23	2.02	−4.18, 3.73
Full	−0.65	2.02	−4.60, 3.31
Ecosystem state × treatment			
Ecotone × large herbivore exclosure	2.01	2.85	−3.58, 7.61
Shrubland × large herbivore exclosure	4.29	2.85	−1.30, 9.89
Ecotone × full exclosure	6.89	2.85	1.30, 12.48
Shrubland × full exclosure	14.31	2.85	8.72, 19.90
Recovery from disturbance			
(Intercept: Grassland, control)	7.70	3.41	1.02, 14.38
Ecosystem state			
Ecotone	−3.64	2.37	−8.30, 1.01
Shrubland	−4.34	2.37	−8.99, 0.31
Treatment			
Large herbivores	2.24	1.67	−1.03, 5.51
Full	4.13	1.67	0.86, 7.41

Note: Herbivore treatments included large herbivore exclosures (cattle and oryx excluded), full exclosures (cattle, oryx, lagomorphs, and rodents excluded), and controls (no herbivores excluded).

Seedling herbivory: Cox model

Seedling survival trials occurred during a particularly dry year in 2023 in which wet season precipitation

FIGURE 3 (a) Conceptual diagram for a structural equation model (SEM) for the influences of shrub cover (state-level, microhabitat), weather, and multiple mammalian herbivore taxa on perennial grass seedling mortality across a shrub encroachment gradient. The direction of pathways is from exogenous (predictor) to endogenous (response) variables. Blue pathways indicate a positive response to predictors, orange pathways indicate negative responses, and gray pathways indicate either positive or negative response dependent on external factors. (b) Results from the top SEM including folivore biomass as the metric for rodents. Significant pathways are shown and include standardized coefficient estimates (Table 2). Image credits: oryx, grass seedling, and rain cloud, Kieran Andreoni; all other images (shrub, woodrat, kangaroo rat, and jackrabbit) are from PhyloPic.org.

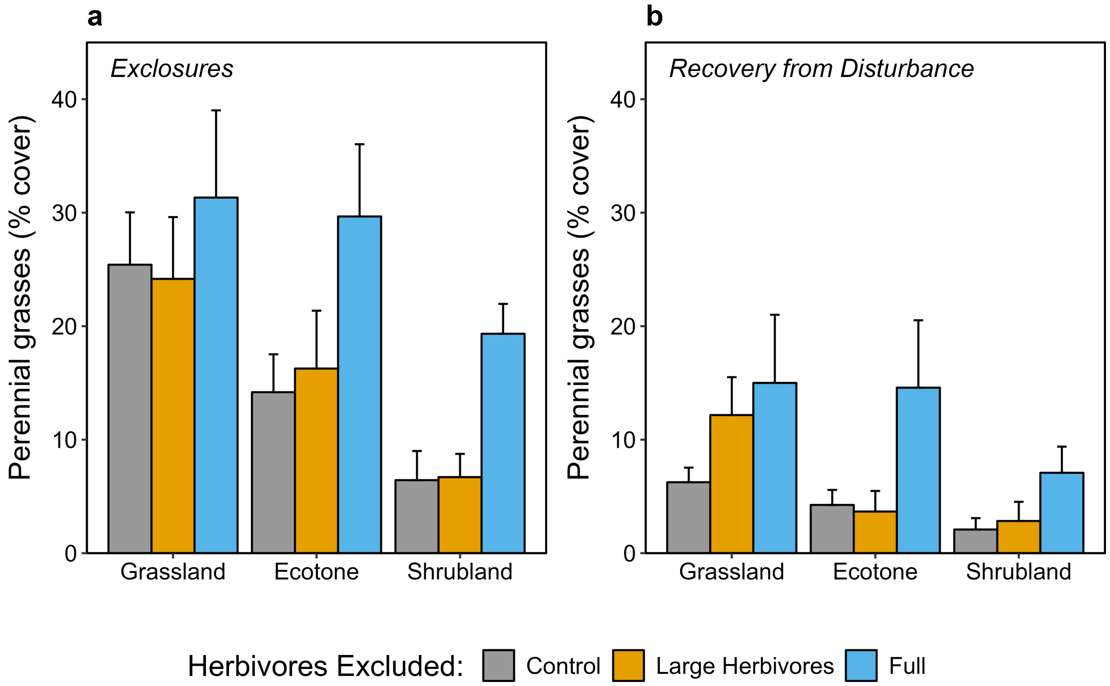

FIGURE 4 Perennial grass cover across ecosystem states within (a) 2 × 2-m herbivore exclosure treatments and control plots and (b) disturbed 40 × 40-cm subplots within treatment and control plots. Exclosures were established in 2001, and disturbance was simulated within subplots through removal of all aboveground plant biomass. Bars represent means for percent foliar cover +1 SE.

(76 ± 7.5 mm; Appendix S1: Figure S2) across our spatial blocks was well below the mean wet season precipitation since the establishment of the Ecotone exclosure study (2001–2023: 137 ± 65.3 mm). This dry period coincided with extreme heat in late July and early August (Appendix S1: Figure S5). By the end of the 15-day trials, 47.1% ± 28.3% of grass seedlings were killed by herbivores.

The Cox proportional hazard model showed that the risk of mortality from herbivory for perennial grasses differed across ecosystem states. In relation to grasslands, seedlings in ecotone (HR = 1.33, 95% CI = 1.12–1.54; $p = 0.009$) and shrubland (HR = 1.55, 95% CI = 1.33–1.77; $p < 0.001$) states were at a higher risk of mortality from herbivory (Figure 5).

Seedling herbivory: Structural equation model

Rodent biomass was moderate during field trials in 2023 compared to long-term population trends (Schooley et al., 2018). Mean rodent biomass was similar among ecological states (609–621 g/ha) with medium granivores and folivores contributing the most biomass (Appendix S1: Figure S3). The large granivore, *D. spectabilis*, was not captured on shrubland and ecotone states, but contributed to rodent biomass on grasslands.

From camera traps, we collected 345 independent detections for black-tailed jackrabbits and 75 independent detections for oryx over 1561 total trap-nights, across 18 camera stations (Appendix S1: Figure S4). Jackrabbits showed no sign of substantial population recovery from rabbit hemorrhagic disease virus compared to estimates from past camera trap (Wagnon et al., 2024) or spotlight (Appendix S1: Figure S6) surveys.

The SEM including rodent folivores produced a better global goodness of fit ($C = 3.80$, df = 6, $p = 0.704$) compared to the SEM including folivores and granivores ($C = 1.89$, df = 2, $p = 0.389$; Appendix S1: Figure S7) or total rodent biomass ($C = 10.44$, df = 8, $p = 0.236$; Appendix S1: Figure S7). Thus, our final SEM (Figure 3b) included pathways from shrub cover (state-level) to rodent folivore biomass and oryx photographic rate. Folivore biomass was positively related to state-level shrub cover ($\beta_{std} = 0.34$), whereas oryx abundance was negatively related to state-level shrub cover ($\beta_{std} = -0.70$; Table 2). However, grass seedling mortality was unrelated to abundances of oryx or jackrabbits, and seedling mortality was negatively related to folivore biomass ($\beta_{std} = -0.23$), which was the opposite of our expectation. Precipitation during trials was not a predictor of grass seedling mortality (Figure 3b). Seedling mortality from herbivory was directly associated with habitat structure at two spatial scales (Figure 3b). Seedling mortality was positively related to state-level shrub cover ($\beta_{std} = 0.12$),

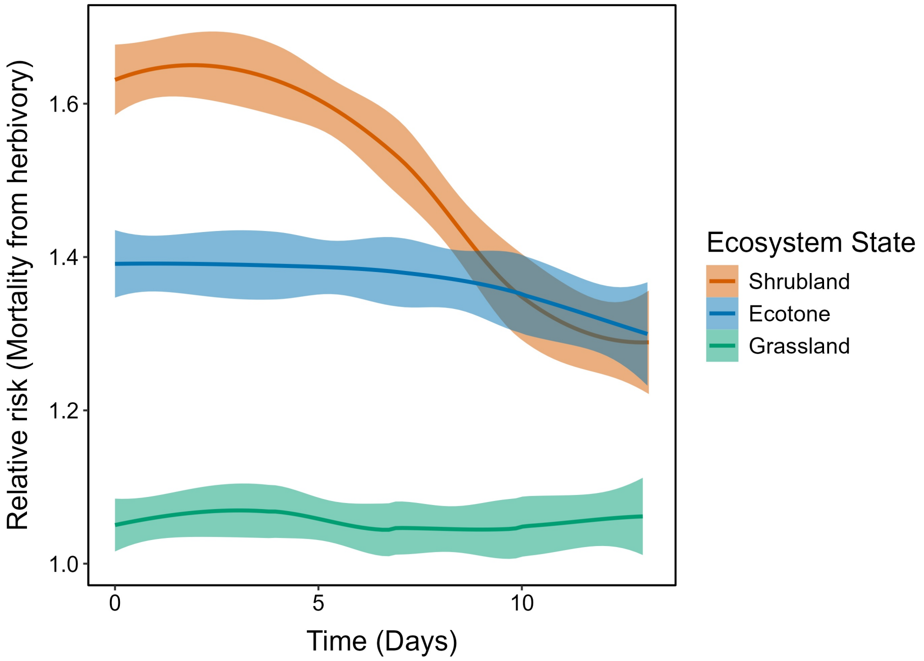

FIGURE 5 Model predictions from the mixed-effects Cox proportional hazard model for the risk of mortality from herbivory for perennial grass seedlings across ecosystem states. Lines indicate the predicted relative risk, and shaded regions indicate the 95% CIs.

TABLE 2 Results from the top structural equation model for perennial grass seedling mortality in response to state-level and microhabitat shrub cover and herbivore pressure.

Response	Predictor	β	SE	df	p	β_{std}
Folivore biomass (g/ha)	Shrub cover (state-level)	6.78	2.88	43	0.023	0.338
Oryx (photographic rate)	Shrub cover (state-level)	−0.009	0.001	43	<0.001	−0.701
Seedling mortality from herbivory	Folivore biomass (g/ha)	−0.005	0.001	41	<0.001	−0.231
	Shrub cover (state-level)	0.053	0.015	41	<0.001	0.125
	Shrub cover (microhabitat)	0.025	0.005	41	<0.001	0.176
Correlated errors						
~~Oryx (photographic rate)	~~Folivore biomass (g/ha)	−0.332	…	45	0.014	−0.332

Note: Rodent folivores included *Neotoma* spp. and *Xerospermophilus spilosoma*. Seedling mortality from herbivory consisted of the proportion of seedlings in trays consumed by the end of field trials. Estimates of coefficients (β) and standardized coefficients (β_{std}) are presented for significant pathways (Figure 3a) and correlated errors.

as well as shrub cover directly surrounding seedlings at the microhabitat scale ($\beta_{std} = 0.18$).

DISCUSSION

With drylands experiencing shrub encroachment globally (Ding & Eldridge, 2023; D'Odorico et al., 2011; Ward, 2016), we need to understand the role of herbivores in such ecosystem state transitions (Gaitán et al., 2018; Kerley & Whitford, 2009). In our study, long-term exclusion of rodents and lagomorphs increased perennial grass cover in ecotone and shrubland states, but not in grassland states. Rodents and lagomorphs also inhibited perennial grass recovery from disturbance across all ecosystem states, although grass patches displayed limited resilience to disturbance. Seedling herbivory was also highest in shrub-encroached states, where habitat structure provided rodents with cover. Overall, small herbivores reduced perennial grass cover, recovery, and seedling survival with the strongest effects in shrub-encroached states. This outcome indicates herbivory by small mammals can function as a feedback, reinforcing grassland–shrubland transitions, but is unlikely to act as a trigger in remnant grasslands.

Our study highlights that long-term studies are crucial to unveiling herbivory effects from native small mammals (Brown & Heske, 1990; Davies et al., 2023;

Maron et al., 2021) because drivers and feedbacks of dryland transformations can be decoupled from their outcomes for decades (Bestelmeyer et al., 2011). Excluding rodents and lagomorphs at our study site produced no noticeable effects on perennial grass cover or recovery after 8 years (Svejcar et al., 2019). Yet, our follow-up survey after herbivores were excluded for 21 years revealed that perennial grass cover on ecotone and shrubland states was two to three times higher in treatment plots excluding rodents and lagomorphs versus control plots. Moreover, these exclusion treatments included some of the only perennial grass patches remaining at our shrubland sites (Figure 1e).

Long-term removal of rodents and lagomorphs improved grass recovery following disturbance across all ecosystem states, indicating that native herbivores can constrain perennial grasses following natural or managed disturbances (e.g., drought, livestock grazing; Gaitán et al., 2018; Gherardi & Sala, 2015; Roth et al., 2009). Grasses recovering from disturbance may be especially sensitive to herbivory (Daleo et al., 2014; Sharp Bowman et al., 2017; Xu et al., 2023), and even small impacts from consumers in low-productivity environments may alter their recovery trajectory (Davies et al., 2023; Hawkes & Sullivan, 2001). Nevertheless, black grama recovery into these disturbed patches was low overall, suggesting that graminivory (Kerley & Whitford, 2009) can have lasting impacts even where surrounding grass cover is high (Seabloom et al., 2020). In fact, only three of the 135 (2.2%) disturbed subplots had >50% perennial grass cover after 21 years, and each of them was in a plot excluding rodents and lagomorphs. Such lasting effects on perennial grasses may explain why it can take many years for herbivory effects to become evident (Farías et al., 2021). Herbivory pressure varies as herbivore populations respond to climate, producing periodic high disturbances that persist and eventually accumulate to strong declines in herbaceous cover over decades.

Herbivory of grasses during the seedling stage is another mechanism that can reinforce shrub encroachment. With the rarity of lagomorphs, rodents drove the mortality of perennial grass seedlings. Thus, the documented pattern of higher seedling herbivory in ecotone and shrubland states (Bestelmeyer et al., 2007) persisted despite the collapse of a major consumer group from disease (Asin et al., 2021; Appendix S1: Figure S7). These results indicate that desert rodents play a major role in habitat-dependent herbivory (Kerley & Whitford, 2009), and feedbacks to ecosystem state change, but lagomorphs amplify these processes in years when they are more abundant (Abercrombie et al., 2019).

Seedling herbivory from rodents was explained best by habitat structure at two scales (Figure 3b). Seedling mortality was related positively to both state-level and microhabitat shrub cover. These two measures of shrub cover are positively related (although not significantly in our dataset), so grassland–shrubland transitions create more foraging spaces with nearby shrubs. Thus, habitat structure may be a better predictor of herbivory pressure than herbivore abundances (Bestelmeyer et al., 2007; Svejcar et al., 2019) if the abundances are above some threshold. Shrubs act as resource islands (Davies et al., 2022; Schlesinger et al., 1990; Thompson, 1987) that may attract herbivores, provide cooler microclimates for diurnal consumers (Levy et al., 2016), and especially conceal rodents from predators (Bowers, 1988; Loggins et al., 2019). Hence, shrub encroachment alters the landscape of fear for consumers, which then translates into an altered landscape of mortality risk for grass seedlings.

Generally, our results are consistent with a different long-term study (25 years) measuring herbivore effects on a grassland at JRN LTER experiencing initial mesquite encroachment (Andreoni et al., 2024). In that study, removal of herbivores had no effect on perennial grass cover for the first decade during a dry period when mesquite cover was low and stable. However, during a subsequent wet period when mesquite expanded, excluding native rodents and lagomorphs increased perennial grass cover. Both studies indicate that altered habitat structure from shrub encroachment promotes positive feedbacks by small mammals, but climate may mediate these processes (Andreoni et al., 2024). Further monitoring of our long-term studies will show whether small mammals also can advance xerification and propel systems toward eroding dune states.

In contrast to native herbivores, cattle and African oryx did not contribute strongly to vegetation dynamics. Cattle grazing is currently light-to-moderate where it occurs across our spatial blocks (Havstad & Bestelmeyer, 2019). However, oryx populations are increasing and their abundances are higher on grassland sites (Andreoni et al., 2021; Appendix S1: Figure S4) where cover of herbaceous forage is high. No estimates exist for oryx population size in the Jornada Basin, but their numbers may be low compared to the carrying capacity of remnant black grama grasslands. Future increases in oryx population size due to predator release in lowlands (Prude & Cain, 2021) could intensify herbivory pressure across remaining grassland ecosystems, functioning as a novel trigger facilitating shrub invasion.

CONCLUSIONS

Native small mammals can exert strong control over perennial grass dynamics, ultimately reinforcing the loss of arid grasslands (Abercrombie et al., 2019; Eldridge et al., 2009; Mallen-Cooper et al., 2019). The conceptual model for grassland–shrubland transitions is expanding beyond the historical triggers of drought and livestock overgrazing as our understanding increases (Bestelmeyer et al., 2018; Pierce et al., 2019). We contend that herbivory from small mammals is a critical biotic feedback that can reinforce regime shifts in drylands. As such, native consumers should be part of the evolving model for state transitions and may be a key reason why the reversal of shrublands to grasslands is rare.

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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: vegetation cover data from herbivore exclosures (Andreoni et al., 2025a): https://doi.org/10.6073/pasta/608df3ba5339af8e9c3091eaa88e2015; grass seedling survival and microhabitat vegetation cover (Andreoni et al., 2025b): https://doi.org/10.6073/pasta/a4efa364823af7512fcf0178f2304f3e; precipitation data from NPP M-WELL site (Anderson, 2023a): https://doi.org/10.6073/pasta/0f2aec22b5c73c426722f408f6956db9; precipitation data from NPP G-IBPE site (Anderson, 2023b): https://doi.org/10.6073/pasta/8a50de5fa8f50fa038a71a0fb302e395; precipitation data from NPP P-TOBO site (Duniway, 2023): https://doi.org/10.6073/pasta/d6428db8a620f176615518c769192ed7; rodent abundance and biomass summaries (Bestelmeyer & Schooley, 2022): https://doi.org/10.6073/pasta/083c12a1452105f7e10bd53861e2e4e3; cattle stocking rates (Havstad & Bestelmeyer, 2019): https://doi.org/10.6073/pasta/c7abcca9658c05a3524f09d064628b6e; mammal camera trap data (Schooley et al., 2024): https://doi.org/10.6073/pasta/56a1ee66420260df555641e970ef1673.

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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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